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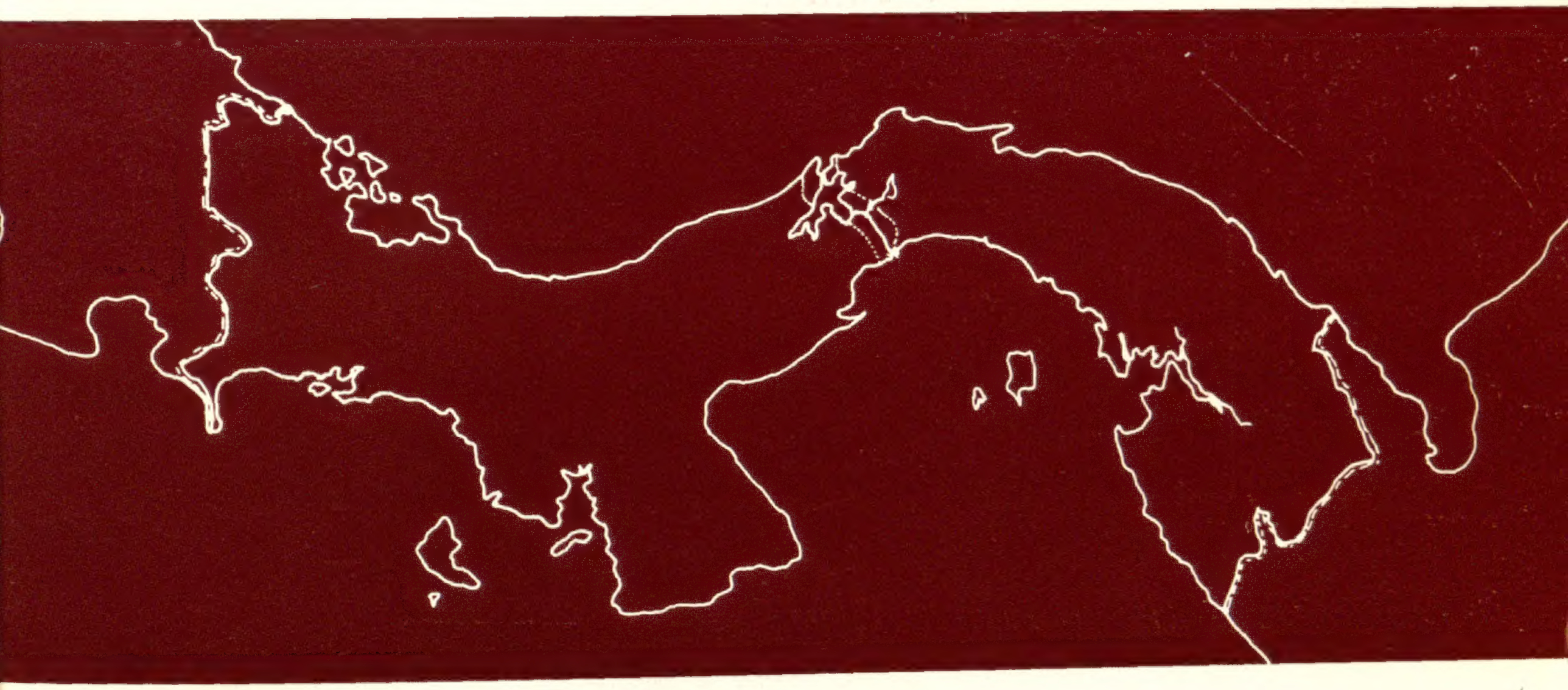

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ANNALS
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VOLUME 62 1975 NUMBER 1

FLORA OF PANAMA[1]

BY ROBERT E. WOODSON, JR. AND ROBERT W. SCHERY
AND COLLABORATORS

Part II

FAMILY 3A. POTAMOGETONACEAE[2]

ROBERT R. HAYNES[3] AND W. ALAN WENTZ[4]

Plants herbaceous, glabrous, annual or perennial, aquatic in fresh, brackish, or saline waters. *Stems* branched or unbranched, usually dimorphic, lower stems rhizomatous and root-bearing, upper stems erect and foliaceous, the tips often hardened into winter buds. *Leaves* submersed and/or floating, alternate or subopposite, 2-ranked, entire or toothed, sessile or petiolate, stipulate, 1- to many-nerved, the stipule forming a tubular sheath around the stem, free or adnate to the leaf base, the nerves parallel, connected by perpendicular cross-veins, submersed leaves thin, linear, or lanceolate, floating leaves often leathery, lanceolate, elliptic, or ovate. *Inflorescence* an axillary or terminal spike or solitary or paired in leaf axils. *Flowers* bisporangiate or monosporangiate (plants then monoecious or less frequently dioecious), the parts arranged in 1–16-merous whorls; perianth absent or if present green, of 4–6 distinct herbaceous segments in one whorl; stamens 1–4, the anthers 1–2-celled, linear, dehiscing vertically; gynoecium of 1–16 distinct carpels, placentation apical or parietal, ovule 1, pendulous. *Fruits* drupaceous or achene-like, opening by decaying of the pericarp, the pericarp usually with a membranous exocarp, fleshy mesocarp, and stony endocarp; seeds

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[1] Assisted by National Science Foundation Grant GB-36202X (Thomas B. Croat, principal investigator).

[2] Contribution from the Department of Botany (Paper No. 865) and the Herbarium of of Ohio State University, Columbus, Ohio 43210.

[3] Department of Botany, 1735 Neil Avenue, Ohio State University, Columbus, Ohio 43210. *Present Address*: Department of Biological Sciences, Louisiana State University at Shreveport, Shreveport, Louisiana 71105.

[4] School of Natural Resources, University of Michigan, Ann Arbor, Michigan 48104.

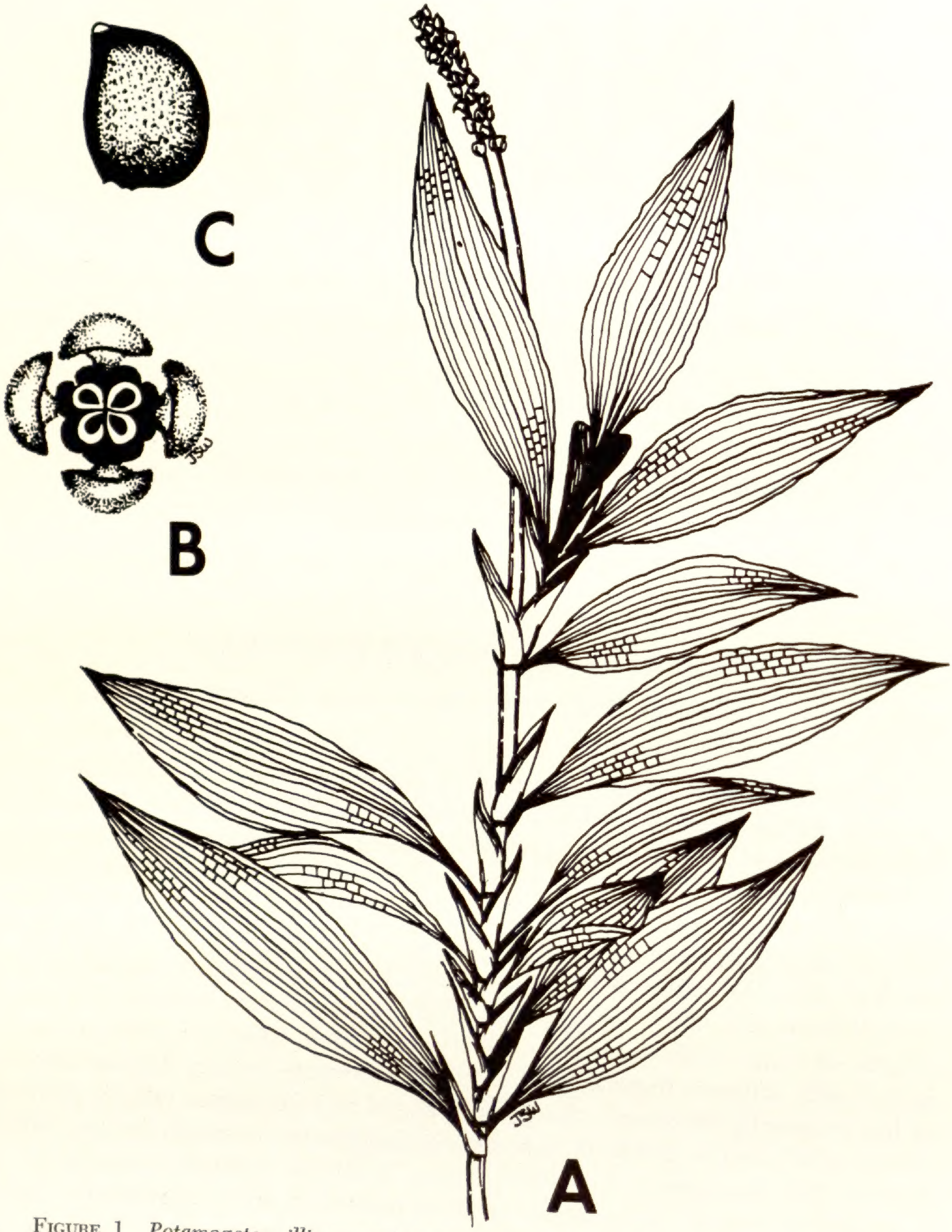

FIGURE 1. *Potamogeton illinoensis* Morong—A. Habit (× ¾).—B. Flower (× 10).—C. Fruit (× 7). [After *Dressler 4184* (OS).]

solitary, pendulous, the embryo straight or curved with a strongly developed hypocotyle, the endosperm absent.

A family of about 8 genera and 120 species, the Potamogetonaceae are widespread in both hemispheres. Four genera, *Halodule*, *Potamogeton*, *Ruppia*, and *Syringodium*, are known to occur in Panama. Members of the family are often important or dominant components of aquatic ecosystems.

a. Flowers monosporangiate; pollen thread-like; carpels 2; plants of saline-water habitats.
  b. Leaves terete or semiterete; flowers in cymes; styles divided into 2 stigmata; anthers attached at same point on filament ..... 4. *Syringodium*
  bb. Leaves flat; flowers solitary; styles with one stigma; anthers attached at different points on filament ..... 3. *Halodule*
aa. Flowers bisporangiate; pollen spherical or bilateral; carpels 4 or more (rarely 2); plants of fresh- or brackish- (rarely saline-) water habitats.
  c. Stamens 2; drupes stipitate; stipules adnate to the leaf base and without a free tip extending past the point of adnation; perianth absent ..... 2. *Ruppia*
  cc. Stamens 4; drupes sessile; stipules free from leaf base or if adnate then with a free tip; perianth present ..... 1. *Potamogeton*

1. POTAMOGETON

Potamogeton L., Sp. Pl. 126. 1753.

Hydrogeton Lour., Fl. Cochinchinensis 244. 1790.
Patamogeton Honckery, Syn. Plan. Germ. 2: 110. 1793.
Potamogiton Raf., Med. Respos. 5: 354. 1808.
Potamogetum Clairville, Man. Herb. Suisse & Valais 34. 1811.
Peltopsis Raf., Jour. Phys. Chim. Hist. Nat. Arts 89: 102. 1819.
Spirillus J. Gay, Compt. Rend. Hebd. Seances Acad. Sci. 38: 703. 1854.

Plants annual or perennial, propagated from seeds, winter buds, or rhizomes, submersed in fresh or rarely brackish water. *Stems* variable in length according to water depth, branched or unbranched, terete or compressed, rooting at the nodes. *Leaves* all submersed and/or floating, alternate or subopposite; submersed leaves pellucid, sessile or petiolate, linear to orbicular, apically subulate to obtuse, basally cuneate to rounded or cordate, the margins entire, the nerves 1–35; floating leaves coriaceous, mostly petiolate, rarely subsessile, elliptic to ovate, acute to obtuse at apex, cuneate to rounded or cordate at base, the margins entire, the nerves 3–51; stipules tubular, sheathing the stem and young inflorescences, connate or convolute, either free or adnate to the base of submersed leaves, free from the base of floating leaves. *Winter buds* present or absent, with extremely shortened internodes, divided into inner and outer leaves; inner leaves few to numerous, unmodified or shortened and oriented at 90° with respect to outer leaves, rolled into a fusiform structure; outer leaves 1–5 per side, mostly similar to vegetative leaves, rarely corrugated near the base. *Inflorescence* a capitate or cylindric spike with 1–20 whorls of flowers, compact or moniliform, with 2–4 flowers in each whorl, mostly buoyed above surface of water at anthesis. *Flowers* bisporangiate; perianth of 4 distinct, rounded, short-clawed, greenish segments; stamens 4, the filaments adnate to the perianth claw, the anthers bithecate, extrorse, pollen spherical, monoaperturate; gynoecium of 4 distinct, unilocular, uniovulate carpels, the placentation parietal, the ovule campylotropus. *Fruit* drupe-like, dorsally rounded or keeled; embryo coiled.

A genus of perhaps 100 species, widespread throughout both hemispheres, especially in temperate and subtemperate regions. One species, *Potamogeton illinoensis*, is known to occur in Panama. Other species, *e.g. P. foliosus* and *P. pusillus*, occur north and south of Panama and may be found in the country. Species of *Potamogeton*, commonly known as "pondweed," are one of the most important food sources of waterfowl and other vertebrates. The plants also pro-

vide cover and breeding areas for many fishes and invertebrates. In some areas, pondweeds occur in such abundance that they are considered troublesome weeds.

Literature:

Fernald, M. L. The linear-leaved North American species of *Potamogeton* section *Axillares*. Mem. Amer. Acad. Arts 17: 1–183. 1932. (Also, Mem. Gray Herb. 3.)

Haynes, R. R. A revision of North American *Potamogeton* subsection *Pusilli* (Potamogetonaceae). Ph.D. Dissertation, Ohio State University. 140 p. 1973. (Also, Rhodora 76: in press.)

Ogden, E. C. The broad-leaved species of *Potamogeton* of North America north of Mexico. Rhodora 45: 57–105, 119–163, 171–214. 1943.

1. **Potamogeton illinoensis** Morong, Bot. Gaz. (Crawfordsville) 5: 50. 1880. —FIG. 1.

Rhizomes buff, spotted or suffused with red. *Stems* simple or branched, terete, 5–60 cm long and 0.2–1.2 mm in diameter. *Leaves* eglandular, dimorphic without lacunae or with up to 2 rows of lacunae on each side of midrib; submersed leaves thin, elliptic to lanceolate, sessile or with petioles to 4.1 cm long, the blades acute to apiculate, 7–17-nerved, 5.7–17 cm long and 1–3.2 cm wide; floating leaves (often absent) more or less coriaceous, elliptic to oblong-elliptic, the petiole 3.2–8.5 cm long, the blades obtuse to apiculate, 11–13 nerved, 4.5–6.2 cm long and 1.5–3 cm wide; stipules light green to dark-brown, persistent, 1.9–6.8 cm long and 1.7–6.1 mm wide, convolute, 2-keeled, free from the blade, divergent and conspicuous. *Winter buds* unknown. *Inflorescence* a cylindrical spike, 2–4.5 cm long and 4.5–8.5 mm in diameter, consisting of 10–16 whorls of flowers, the whorls 1.5–5 mm apart; peduncles cylindric, erect, terminal, 4.8–16.2 cm long and 2.5–3.8 mm wide. *Fruits* olive-green to brownish, dorsally and laterally keeled, 2.2–2.7 mm long and 2.1–2.5 mm wide, keels without undulations, ridge-like, the dorsal keels 0.2–0.3 mm high, the lateral keels less developed but often with a projecting basal knob, beak (0.1–)0.3–0.6 mm long, 0.2–0.5 mm in diameter, sides flat, wall texture slightly reticulate.

This species occurs in rivers and ponds from southwestern Quebec to southern British Columbia, south to Florida, West Indies, Texas, California, Mexico, and Central America.

PANAMÁ: Laguna east of El Valle de Antón (prov. Coclé), *Dressler 4184* (OS).

2. RUPPIA

Ruppia L., Sp. Pl. 127. 1753.

Plants herbaceous, submersed in brackish or saline waters, annual or perennial, propagating from seeds, rhizomes, or winter buds. *Stems* variable in length according to water depth, branched or unbranched, terete, rooting at the nodes. *Leaves* all submersed, sub-opposite or alternate, linear or setaceous, uninervate, with a stipular sheath at the base, apex acute to truncate, margins entire throughout or minutely serrulate at the apex; stipule adnate to leaf base for its entire

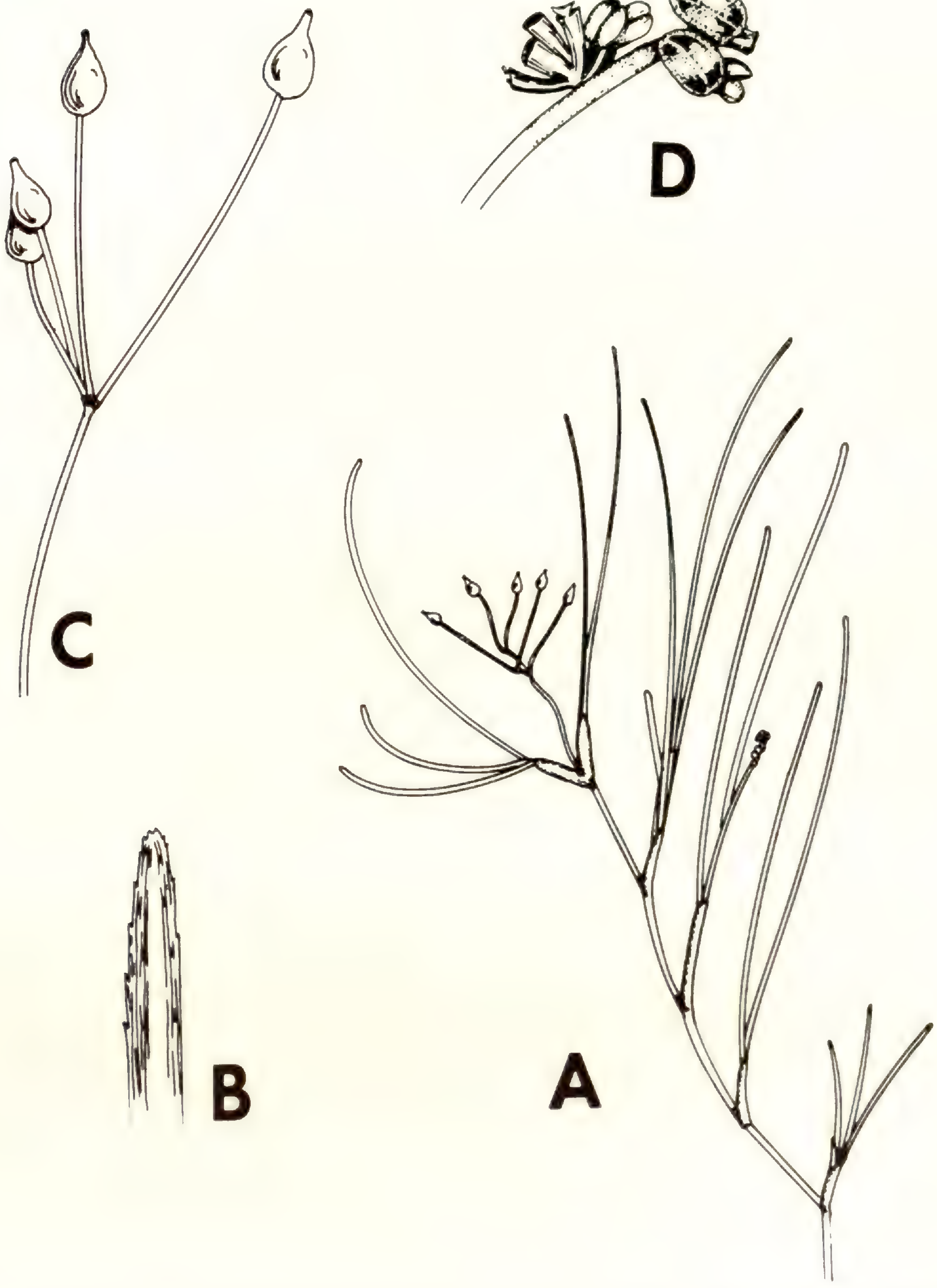

FIGURE 2. *Ruppia maritima* L.—A. Habit (× ¾).—B. Leaf apex (× 66).—C. Inflorescence in fruit (× 7).—D. Inflorescence in flower (× 6¼). [After *McDaniel 8019* (DUKE).]

length. *Winter buds* present or absent, with one internode, the leaves undifferentiated. Inflorescence a 1- to few-flowered capitate spike enclosed in a spathe-like sheath; peduncle elongating at anthesis, elevating the inflorescence to or near the water's surface. *Flowers* bisporangiate; perianth absent; stamens 2, sessile; carpels 2–16, distinct, stipitate, placentation parietal, ovule one. *Fruits* drupaceous, dorsally rounded, each on a short stipe which usually elongates after anthesis.

Ruppia is a cosmopolitan genus of perhaps six species; one species, *Ruppia maritima*, is known to occur in Panama. *Ruppia*, commonly known as "Widgeon-grass," is an important food and cover source for many waterfowl and invertebrates.

1. **Ruppia maritima** L., Sp. Pl. 127. 1753.—FIG. 2.

Rhizome 0.2–0.4 mm wide, the internodes to 1.5 cm long. *Stems* to 1 m long, 0.3–0.6 mm in diameter, erect. *Leaves* to 1 dm long; sheaths 7–14.5 mm long and to 1.1 mm wide; blades 0.2–1.0 mm wide, 1-nerved, the apex acute with several minute teeth. *Winter buds* absent. *Inflorescence* a 2-flowered spike. *Flowers* with anthers 0.5–0.7 mm long and 0.5–0.6 mm wide; carpels 4–5, ca. 0.5 mm long and ca. 0.1 mm wide. *Fruits* 1.2–1.9 mm long and 0.7–1.2 mm wide, beak 0.6–0.8 mm long, stipe 2–6.5 mm long and ca. 0.2–0.4 mm wide.

In brackish and saline waters throughout the world.

HERRERA: Cienaga El Mangle, NE of Paris, *McDaniel 8019* (DUKE). PANAMA: near beach at Nueva Gorgona, *Duke 4525* (MO).

3. HALODULE

Halodule Endl., Gen. Pl. Suppl. 1: 1368. 1841.

Diplanthera Thouars, Gen. Nov. Madag. 2: 3. 1806, non Gleditsch, 1764.

Plants herbaceous, glabrous, perennial, submersed in saline water, dioecious. *Rhizomes* creeping, simple or branched, with one or more roots and a short erect stem at each node. *Stems* with 1–4 leaves and subtended by scarious elliptic or ovate scales. *Leaves* alternate or appearing opposite because of reduced internodes, sessile, divided into a blade and a sheath; sheath persisting longer than the blade, leaving a circular scar when shed; blades linear, compressed, terete, entire except apically, often narrowed at the base, 3-nerved, the midrib conspicuous, the lateral nerves inconspicuous, each ending in a tooth, the apex 2–3 toothed. *Flowers* terminal, solitary, each enclosed in a leafy bract; perianth absent; staminate flowers stalked consisting of 2 anthers attached to the filament at different levels and joined dorsally at their base, the anthers 4-thecate, dehiscing vertically; carpellate flowers subsesssile, consisting of two distinct uniovulate carpels, each carpel with a distinct style. *Fruits* achene-like with a stony pericarp, slightly compressed, subglobose to ovoid, with a short beak.

A genus of perhaps five species *Halodule* is widely distributed along the shores of tropical and sub-tropical oceans in both hemispheres. One species, *Halodule wrightii*, is known to occur in Panama.

Literature:

Hartog, C. Den. An approach to the taxonomy of the sea-grass genus *Halodule* Endl. (Potamogetonaceae). Blumea 12: 289–312. 1964.

———. The Sea-Grasses of the World. North-Holland Publishing Co., Amsterdam. 275 pp. + 31 pl. 1970.

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Phillips, R. C. On species of the seagrass, *Halodule*, in Florida. Bull. Mar. Sci. Gulf & Caribb. 17: 672–676. 1967.

Wentz, W. A. & R. L. Stuckey. The changing distribution of the genus *Najas* (Najadaceae) in Ohio. Ohio Jour. Sci. 71: 292–302. 1971.

1. **Halodule wrightii** Aschers., Sitzber. Ges. Fr. Berlin 19. 1868.—Fig. 3.

Diplanthera wrightii Aschers. *in* Engler & Prantl, Pflanzenfam. Nachtr. 2: 37. 1897.
D. ciliata Hartog, Pacific Naturalist 1: 15. 1960.
D. beaudettei Hartog, Pacific Naturalist 1: 15. 1960.
Halodule beaudettei (Hartog) Hartog, Blumea 12: 303. 1964.
H. ciliata (Hartog) Hartog, Blumea 12: 309. 1964.

Rhizomes round, 0.3–2 mm in diameter, the internodes 0.4–3.5 cm long. *Stems* erect, to 3.5 cm long; scales elliptic, 0.4–0.5 mm long. *Leaves* linear; sheath 1–4 cm long and 0.5–2 mm in diameter; blade 1.9–20 cm long and 0.2–1.5 mm wide, narrowed at base, the midrib conspicuous and usually excurrent in a small tooth, the lateral nerves inconspicuous but often ending in a tooth longer than the median tooth, apex bicuspidate to tricuspidate. *Flowers* and *fruits* not seen (for description of flowers and fruits, see Hartog, 1964).

Hartog (1964) recognized three species of *Halodule* (*H. beaudettei*, *H. cilata*, and *H. wrightii*) from the coasts of Panama. The species were differentiated by the leaf tip morphology. However, Phillips (1967) demonstrated that leaf tip variation within a single population of *Halodule* in southern Florida fully encompassed the morphological ranges of all three taxa. Phillips concluded that, at least in southern Florida, *H. beaudettei* should be included in *H. wrightii*.

Our examination of other genera of aquatic plants (Haynes, 1973; Wentz & Stuckey, 1971) has also demonstrated great morphological variability within individual taxa. For this reason, and since flowers and fruits of *H. beaudettei* and *H. ciliata* are unknown (Hartog, 1970), we have elected to include these two names under *H. wrightii*.

COLÓN: Colón, *Howe s. n.* (NY). PANAMÁ: Taboga, *Mortensen* s. n. (MO, US).

4. SYRINGODIUM

Syringodium Kutz. *in* Hohenacker, Alg. Marine Sicc. 9, no. 426. 1860.

Cymodocea C. Konig sect. *Phycoschoenus* Aschers., Linnaea 35: 162. 1868.
Cymodocea C. Konig subgen. *Phycoschoenus* (Aschers.) Aschers. *in* Neumayer, Anl. Wiss. Beob. Reisen 363. 1875.
Phycoschoenus (Aschers.) Nakai, Ord. Fam. 211. 1943.

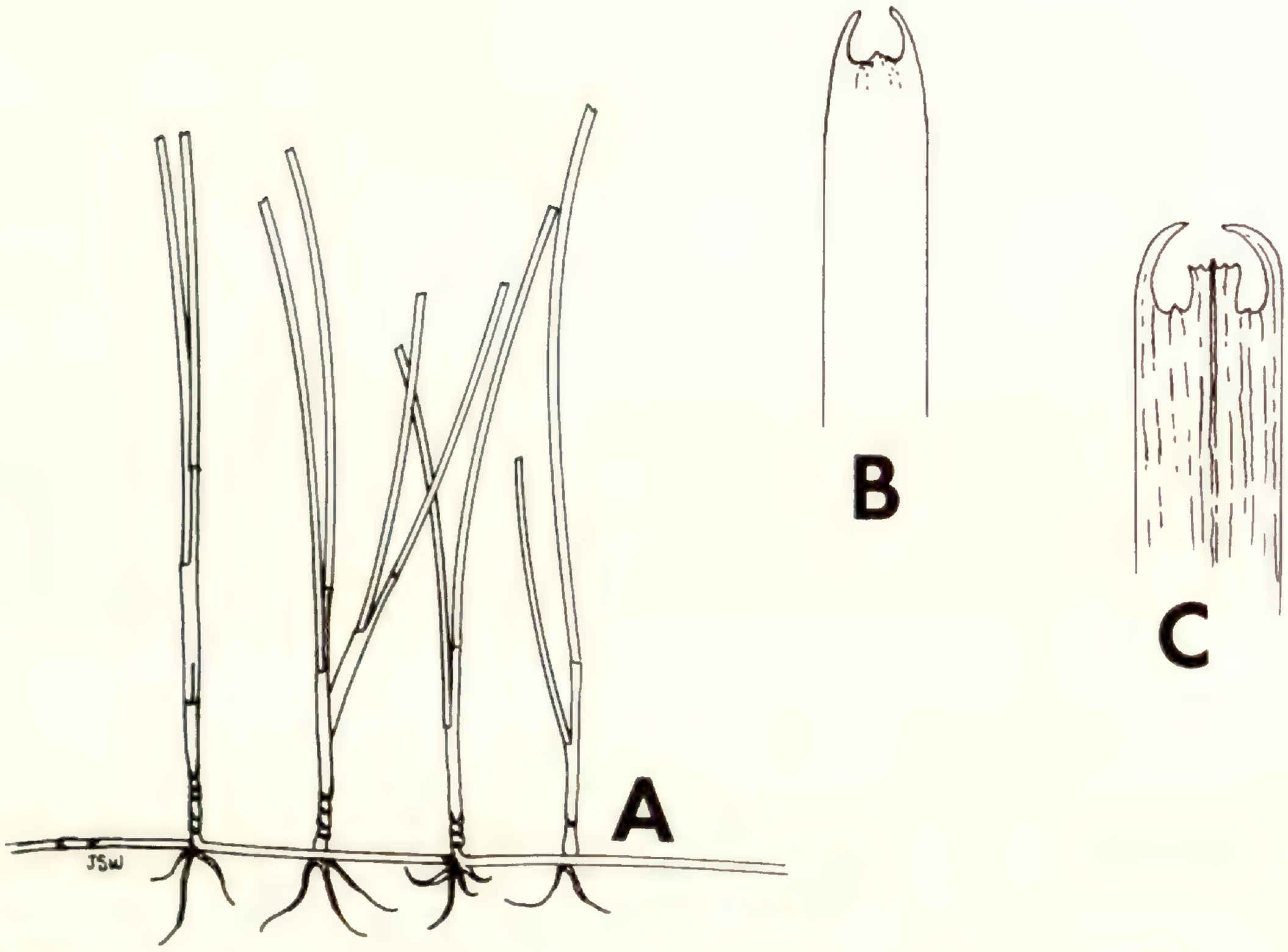

FIGURE 3. *Halodule wrightii* Aschers.—A. Habit (× ½).—B. Bidentate leaf apex (× 38½).—C. Tridentate leaf apex (× 28). [After *Mortensen s.n.* (MO).]

Plants herbaceous, perennial, submersed in saline water, dioecious. *Rhizomes* creeping, monopodial, with one or more roots and a short erect stem at each node. *Leaves* 2–3 on each stem, divided into a sheath and a blade; sheath broad, persisting longer than the blade, leaving open circular scars when shed, bi-auriculate, stipulate, the auricules obtuse; blades linear, often narrowed at the base. *Inflorescence* cymose, the lower branches dichasial, the upper monochasial. *Flowers* axillary to a reduced leaf, the sheath of which is inflated; perianth absent; staminate flowers stalked, each consisting of 2 anthers dorsally connate at their lower parts and attached at the same height on the stalk; carpellate flowers sessile, each consisting of 2 distinct ovaries, each with a short style which divides into 2 long stigmata. *Fruits* achene-like with a stony pericarp, ellipsoid to obovoid, quadrangular in cross section and with an inconspicuous dorsal median ridge.

A genus of two species, *Syringodium* is restricted to the Caribbean Sea and the Indian and western Pacific Oceans. One species, *Syringodium filiforme*, is known to occur in Panama.

Literature:

Hartog, C. Den. The Sea-Grasses of the World. North-Holland Publishing Co., Amsterdam. 275 pp. + 31 pl. 1970.

FIGURE 4. *Syringodium filiforme* Kutz., habit sketch with flowering branch (× ½). [After *Elmore L38* (US).]

1. **Syringodium filiforme** Kutz. *in* Hohenacker, Alg. Marine Sicc. 9, no. 426. 1860.—FIG. 4.

Cymodocea filiforme (Kutz.) Correll, Wrightia 4: 74. 1968.
C. manatorum Aschers., Sitzber. Ges. Fr. Berlin 19. 1868.

Rhizome round, 1.5–3.5 mm in diameter, the internodes 1.5–4 cm long. *Stems* erect, to 1 cm long; scales elliptic, 2–4 cm long. *Leaves* linear; sheath 1.2–6.8 cm long and 2–3.7 mm in diameter; blade 10–30 cm long and 0.5–2.2 mm wide, slightly narrowed at the base. *Inflorescences* in bract axils, 2–7 cm long. *Flowers* solitary, the bract 5–9.5 mm long; staminate flowers consisting of 2 anthers 3–4.5 mm long attached to a stalk, the stalk elongating to 5 mm at anthesis; carpellate flowers with ovaries to 4.5 mm long, the style to 2.5 mm long, the stigmas to 3.5 mm long. *Fruits* 5.5–6 mm long and 3–4.5 mm wide, 4-angled with a conspicuous dorsal keel, the lateral surfaces centrally convex.

SAN BLAS: Caledonia Harbor, Mt. Vernon, *Elmore L38* (NY, UC, US).

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FLORA OF PANAMA[1]

BY ROBERT E. WOODSON, JR. AND ROBERT W. SCHERY
AND COLLABORATORS

Part V

FAMILY 80A. BRUNELLIACEAE

DUNCAN M. PORTER[2] AND JOSÉ CUATRECASAS[3]

Evergreen *trees*; trunks tall, unarmed, the terminal branching dichasial. *Leaves* opposite or ternate, simple or pinnate, coriaceous or subcoriaceous, mostly pubescent, the margins mostly dentate; stipels present on the rachis in compound leaves; stipules lateral, 1 or 2 pairs on each side of the leaves or verticillate, free. *Inflorescences* determinate or definite and dichasial, axillary on young and terminal branchlets, usually large cymose panicles, commonly pubescent, rarely glabrous. *Flowers* small, basically actinomorphic or 4-, 5-, 6(–8)-merous, bisexual or mostly unisexual by abortion and the plants dioecious; sepals connate basally, ovate or ovate-triangular, valvate, persistent; petals absent; stamens usually twice as many as the sepals, in 2 or rarely more whorls, inner whorl opposite the sepals, reduced to short sterile staminodes in carpellate flowers, the filaments free, hirtellous, inserted below and outside the disc margin, the anthers ellipsoid, bilobed, each lobe 2-thecate, oscillating or pendulous, introrse, longitudinally dehiscent; intrastaminal disc thick, flat or concave, pubescent, 10–12(–24)-notched, with as many indentations as stamens or staminodes; gynoecium apocarpous, the carpels free, immersed basally in the disc, the same number or fewer than the sepals and alternate with them, rudimentary in staminate flowers, the ovaries ovoid or ellipsoid, apiculate, commonly densely pubescent and mostly hispid, 1-loculed, the ovules collateral, anatropous, epitropous, 2 per locule, the stylodia subulate, erect in flower, more or less rigid, hooked or curved apically, the stigmas linear, sutural. *Fruit* a stellate polyfollicle; follicles the same number as sepals or fewer, ovoid or ellipsoid, apiculate, tomentulose and usually also hispid or hirsutulous with stiff prickly bristles, the stylodia diverging horizontally and radially; endocarp cartilaginous or corneous, detaching at maturity and expelling the seeds; seeds 1 or 2, ellipsoid, the raphe conspicuous, the testa hard, shining, the episperm firm, thick, cartilaginous, the endosperm abundant, fleshy, white, the embryo straight, the cotyledons flat, the radicle superior.

A tropical American family of trees of humid forests, containing one genus

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[1] Assisted by National Science Foundation Grant GB-36202X (Thomas B. Croat, principal investigator).

[2] Systematic Biology Program, National Science Foundation, Washington, D.C. 20550.
[3] Department of Botany, Smithsonian Institution, Washington, D.C. 20560.

ANN. MISSOURI BOT. GARD. 62: 11–14. 1975.

FIGURE 1. *Brunellia darienensis* Cuatr. & Porter.—A. Habit (× 2/5).—B. Infructescence (× 1⅜).—C. Fruit (× 5).—[After *Duke & Elias 13850* (US, isotype).]

and 52 species and occurring in southern Mexico, Central America, the West Indies, and Andean South America from Venezuela to Bolivia.

At fruit dehiscence, the seed is expelled from the follicle through contraction of the endocarp. It remains attached and dangling by a flexuous placental stalk

that continues the funiculus. The shiny brownish or reddish seeds presumably then are eaten and dispersed by birds.

Literature:

Cuatrecasas, J. Brunelliaceae. Fl. Neotropica, Monogr. 2: 1–189. 1970.

1. BRUNELLIA

Brunellia Ruiz & Pav., Prodr. Fl. Peru. 71. 1794.

Apopetalum Pax, Repert. Nov. Sp. 5: 226. 1908.

Characters of the family.

1. **Brunellia darienensis** Cuatr. & Porter, Phytologia 26: 485–486. 1973. TYPE: Panama, *Duke & Elias 13850* (MO, holotype; US, isotype).—FIG. 1.

Small *tree*; terminal branches leafy, dark green, subterete, slightly or inconspicuously striolate, glabrescent, the branchlets of this year's growth green, flattened, striate, slightly puberulent. *Leaves* opposite, odd-pinnate, pubescent, 16–34 cm long; petioles gradually enlarging basally, adaxially more or less sulcate, otherwise slightly striolate, 5.5–11 cm long; rachis for the most part narrowly sulcate, keeled distally, the interjuge 2.5–4.5 cm long; stipels paired, moderately thick, subulate, acute, sparingly pilosulous, ca. 2 mm long; leaflets 11–15, elliptic-oblong, acuminate and attenuate apically, asymmetrical and obtuse basally, chartaceous, the margin simply crenate-serrate, the teeth ascending, obtuse, callose, minute, mostly 8–12 mm apart, the blade adaxially somewhat smooth, shiny, slightly puberulent, the midvein and secondary veins prominulent, conspicuously of another color than the lamina, abaxially dull, moderately pubescent, conspicuously so at the veins, the midvein pale yellow, well-elevated, the secondary veins 13–15 per side, pale yellow, prominent, parallel and ascending at a 40–50° angle, slightly curved, terminating in the callosaties of the marginal teeth, the lateral leaflets 10–15 cm long and 3–4.2 cm wide, the basals 8 cm long and 2.5 cm wide, the acumens subulate, acute, 1.5–2 cm long, the petiolules dilated basally, sulcate above, slightly puberulent, the laterals 5–6 mm long, the terminal 12–20 mm long; stipules paired, lanceolate-acuminate, pubescent apically, 4–5 mm long and 1 mm wide basally. *Panicles* cymose, to 15 cm long and 7 cm wide in fruit, the branches slender, flattened, striolate, spreading, sparsely puberulent; pedicels terete, slender, rigid, sparsely subadpressed-puberulent, 2–4 mm long, articulated with the branches; bracteoles caducous, absent. *Flowers* 5-merous, bisexual; calyx expanding in fruit to ca. 6 mm in diameter, the lobes ovate, acute, adaxially minutely papillose-strigose apically and on the margin, abaxially minutely and sparsely strigose-puberulent, 2–2.2 mm long and 1.5–1.7 mm wide; stamens with the filaments dilated basally, densely hispidulous, 2–2.5 mm long, the anthers 0.5 mm long; ovary densely sericeous, the trichomes antrorse, longer apically. *Follicles* ovoid-ellipsoid, slightly compressed, apiculate, 3 mm long and 2.5 mm wide, minutely pubescent, the trichomes somewhat longer apically, spreading-ascending, the proximal part of

the stylodium persisting, rigid, spreading, 1–1.5 mm long, often all 5 developed and forming a stellate polyfollicle 5 mm in diameter at maturity; endocarp ellipsoid, cartilaginous, punctate, insertion obtuse, 2 mm long and 1.8 mm wide, 1.5 mm thick, open U-formed when dry; seeds 1 per follicle, ellipsoid-ovoid, somewhat compressed, shining, brown, 1.8 mm long and 1.6 mm wide, 1.2 mm thick

Endemic to Panama, this species fruits in August.

Brunellia darienensis is known only from the type collection, but it is to be expected elsewhere in the higher elevations of eastern Darién.

DARIÉN: Cerro Pirre, cloud forest, 2500–4500 ft, *Duke & Elias 13850* (MO, holotype; US, isotype).

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FLORA OF PANAMA[1]

BY ROBERT E. WOODSON, JR. AND ROBERT W. SCHERY
AND COLLABORATORS

Part VI

FAMILY 86. TROPAEOLACEAE

BENKT SPARRE[2]

Annual or perennial *herbs*, mostly climbers, rarely procumbent terrestrials; subterranean part, if perennial, sometimes a rhizome or a tuber. *Leaves* alternate, stipulate; stipules mostly small and caducous; petioles long, normally of the same length as the lamina or longer, rarely shorter; lamina entire, lobed or palmately divided, peltate or subpeltate. *Flowers* normally single, in 2 species umbellate or fasciculate, appearing at the base of the leaves; peduncles mostly long, ebracteolate (except one species); calyx 5-lobed ending in an elongate, or sometimes short, spur, sepals 5, all alike or sometimes the inferior 2 larger; petals 5, 2 free, inserted at the base of the sepals, entire, serrate or lobed, eciliate or ciliate; stamens 8; pistil simple with a 3-lobed stigma, ovary 3-locular. *Fruit* a schizocarp with 3 indehiscent carpels.

The Tropaeolaceae is a small family of 3 genera, 2 of which are endemic in Patagonia and contain together 3 species. In Panama only *Tropaeolum* occurs, which in total contains 86 species and ranges from southernmost Mexico to southeastern Brazil and Patagonia.

Literature:

Sparre, B. Monograph of the Family Tropaeolaceae. Opera Botanica, Ser. A (in press).

1. TROPAEOLUM

Tropaeolum L., Sp. Pl. 345. 1753; Gen. Pl., ed. 5. 162. 1754.

Description as for the family.

The two aberrant Patagonian genera differ in having either erect peduncles and an almost actinomorphic calyx (*Trophaeastrum*) or in having winged carpels, samaras (*Magallana*).

In Panama 4 species occur, 2 of which are introduced as ornamentals. One other species included here, *T. moritzianum*, Costa Rica and Colombia, has been confounded with *T. emarginatum* (see below). The species grown as ornamentals are known as "nasturtiums" (not related to the genus *Nasturtium*, Cruciferae).

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[1] Assisted by National Science Foundation Grant GB-36202X (Thomas B. Croat, principal investigator).

[2] Swedish Museum of Natural History, Section for Botany, S-104 05 Stockholm 50, Sweden.

a. Receptacle not elongating, *i.e.* ripe carpels not on a carpophore; spur straight; petals entire at base.
  b. Leaves with 5 or more principal nerves, the middle three unforked; inferior petals ciliate at the base of the lamina.
    c. Petals entire or undulate, not ciliate at apex; superior petals of the same size or bigger than the inferior petals ..... 1. *T. majus*
    cc. Petals ciliate; inferior petals bigger or at least longer than the superior petals ..... 2. *T. moritzianum*
  bb. Leaves with 3 principal nerves, the lateral ones forked; inferior petals not ciliate at laminar base or stipe.
    d. All petals serrate-ciliate at apex, more or less of the same size ..... 3. *T. emarginatum*
    dd. Superior petals not ciliate, about half the size of the interior petals, subentire ..... 4. *T. pendulum*
aa. Receptacle elongating, ripe carpels on a carpophore; spur conspicuously hooked; interior petals notably smaller than the superior petals, and with a big tooth at the base ..... 5. *T. peregrinum*

1. **Tropaeolum majus** L., Sp. Pl. 345. 1753.—FIG. 1.

Climbing or prostrate annual *vine*, often stout or almost fleshy, normally glabrous. *Leaves* rarely somewhat pubescent at base; petioles to 15–20 cm long; laminae large, to 10 by 10 cm or more, suborbicular, peltate with 7–11 unforked principal nerves, the margin entire or undulate, the apex in adult leaves not mucronate. *Flowers* single; peduncles of the same length as the petioles or shorter; calyx lobes lanceolate, acute, 15–18 mm long, basally 8–9 mm broad, the superior lobes somewhat smaller, like the spur often yellowish green or green; spur stout, inflated in the lower half, darker apically, slightly curved, 25–35 mm long; superior petals cuneate, somewhat undulate, emucronate, 30–40 mm long, inferior petals unguiculate, ciliate, the blade 15–20 by 15–20 mm, the claw 12–15 mm long, nerves and maculation from light lemon to blackish purple. Fruiting *carpels* to 10 mm long, fleshy, with rugose ribs.

This species is cultivated and sometimes escapes. It is probably of hybrid origin, and is not known in the wild. It was brought to Europe from Peru in 1684.

"Capuchina," "espuela del gelan."

2. **Tropaeolum moritzianum** Klotzsch, Allg. Gartenz. 6: 241. 1838.—FIG. 2.

Stout annual *climber*, to 10 m long, in all parts glabrous. *Leaves* with small, persistent stipules; petioles to 15 cm, pendant, reddish; lamina orbicular to suborbicular, 3.5–9 cm long and 4–11 cm broad, normally glaucescent below, slightly 5–7-lobed to sublobate, the lobes obtuse to subacute, mucronulate or emucronate, peltate, the base slightly concave or subtruncate, rarely somewhat convex, principal nerves 5, the middle 3 unforked. *Flowers* on long (somewhat longer than the petioles) peduncles, these often reddish; calyx lobes homomorphic, elliptic, subacute, 10–12 mm long and 4–5 mm broad, like the base of

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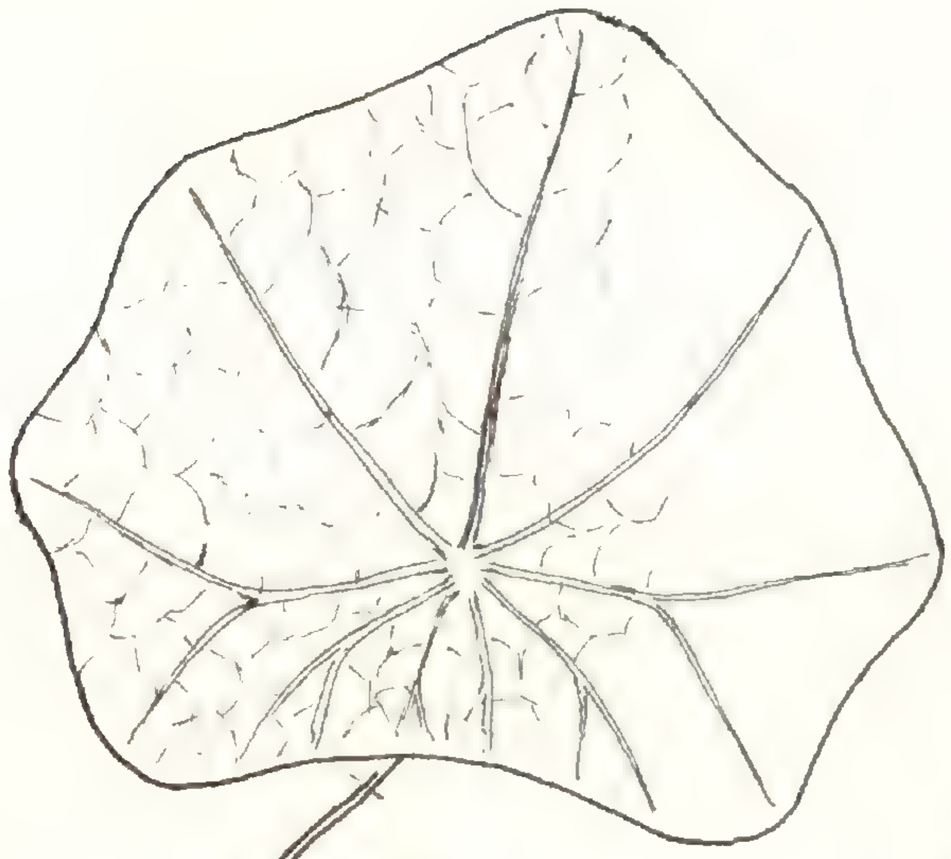
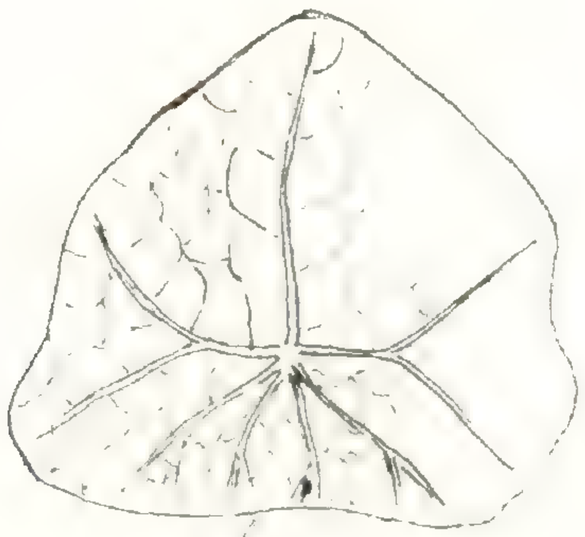
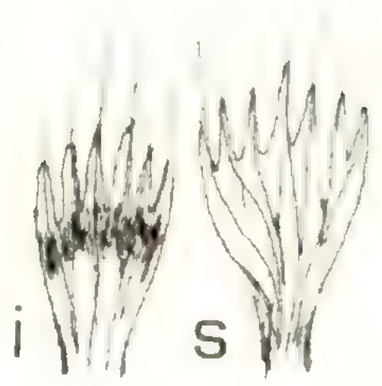
FIGURES 1–5. *Tropaeolum*: i = inferior petal (× 2⅔); s = superior petal (×2⅔); → leaves and flowers, × ⅘.—1. *T. majus* L.—2. *T. moritzianum* Klotsch.—3. *T. emarginatum* Turcz.—4. *T. pendulum* Klotsch.—5. *T. peregrunum* L.







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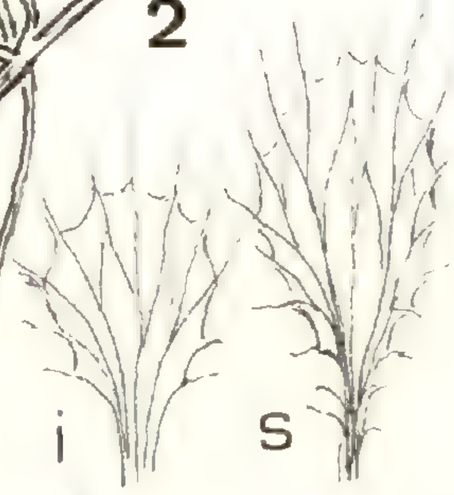

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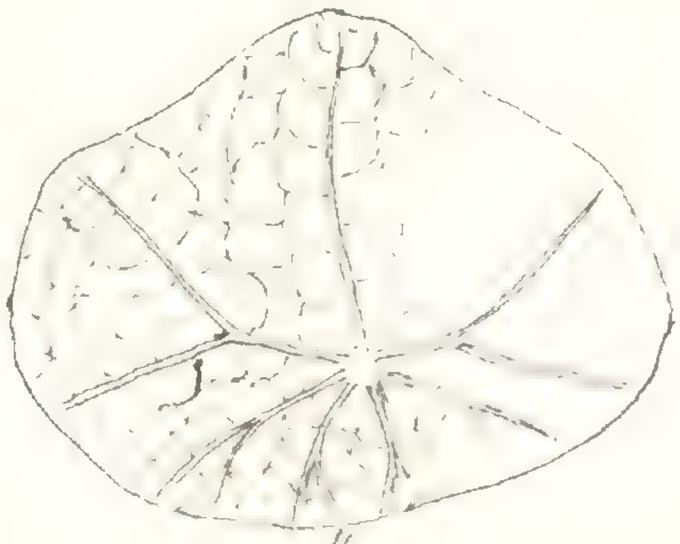

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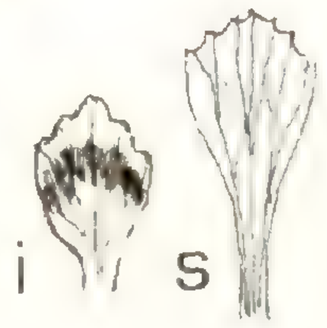

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the spur red or crimson, sometimes greenish at the tips; spur 20–25 mm, straight or somewhat curved upwards, basally conical and with a slender greenish apex; petals yellow, orange or reddish, the nerves red or purplish giving the petals a reddish image, serrate-ciliate apically and laterally, the upper petals cuneate to spathulate (or broadly unguiculate), 8–9 mm long, 4–5 mm broad near the apex, the lower petals long-unguiculate, 10–12 mm long with ciliate stipe, the lamina 7 mm long, 4–5.5 mm broad. Fruiting *carpels* large, 10 mm, triangular, ribbed.

Not known from Panama, but ranging from Guatemala to Costa Rica and known also from Colombia and Venezuela, this species is often confused with *T. emarginatum* (see below).

3. **Tropaeolum emarginatum** Turcz., Bull. Soc. Imp. Naturalistes Moscou 31(1): 425. 1858. TYPE: Panama, *Warscewicz 4–14* (B, holotype, destroyed, photo Field 12665; G, Isotype; K, fragments of type collection).—FIG. 3.

T. bimaculatum Klotzsch *ex* Buch., Bot. Jahrb. (Syst.) 15: 217. 1892.
T. moritzianum, sensu auct., non Klotsch.
T. guatemalense Suess., Fedde Repert. 51: 205. 1942.

Tall, probably annual *climber* to 8 m long, glabrous or rarely (juvenile) sparsely pubescent around the base of the petioles; stipules small, usually persistent; petioles 6–9 cm. *Leaves* dark green, somewhat glaucescent below, suborbicular, 3–6 cm long, 4–7 cm broad, 5-lobed to sublobate, the lobes obtuse, emucronate, peltate, the principal nerves 3, the lateral nerves forked. *Flowers* on slender, often reddish peduncles, shorter than the petioles or of the same length; calyx lobes homomorphic, elliptic to almost suborbicular, 9–10 mm long, 7 mm broad, subacute, reddish or sometimes somewhat greenish yellow; spur 20–25 mm long, straight or slightly curved, the base conical to cylindrical, 12–15 mm long, abruptly turning in a slender appendix, normally red but sometimes greenish near the apex; petals serrate-ciliate, yellow, the upper petals cuneate to spathulate, 8–9 mm long, 4 mm broad near the apex, often with a purple spot, the lower petals long unguiculate, 10–11 mm long, the lamina 5–6 mm long, 4–5 mm broad, not spotted. Fruiting *carpels* triangular, 5–6 mm long, ribbed.

This species ranges from southernmost Mexico (Chiapas) to Colombia.

Apparently the name *T. emarginatum* was not at first taken seriously, and Buchenau and later Suessenguth, described the species anew. The nervation character separates this species from *T. moritzianum*.

In the same alliance, Buchenau also described *T. warscewiczii* (Bot. Jahrb. (Syst.) 26. 582. 1899.) from "Costa Rica et Veragua" based on *Warscewicz 2-15* (B, destroyed, photo Field 12683; G, K, isotypes). The material is too poor to make a firm decision. According to Buchenau's drawing of the petals, the species is probably related to the continental South American *T. fintelmannii* Wagen *ex* Schlecht.

BOCAS DEL TORO: Robalo trail, northern slopes of Cerro Horqueta, 6000–7000 ft, *Allen 4930* (F, G, MO). CHIRIQUÍ: "Chiriqui & Carthaga Vulkan," *Warscewicz 4-14* (G, K). Cerro Punta, 6025 ft, *White 199* (GH, MO, US). Near Cerro Punta, *White 31* (GH, MO).

Vicinity of "New Switzerland," central valley of Río Chiriquí Viejo, 1800–2000 m, *Allen 1390*, (F, GH, MO, NY, US).

4. **Tropaeolum pendulum** Klotzsch, Allg. Gartenz. 18: 377. 1850.—Fig. 4.

Apparently an annual, tall and slender *climber*, 5–8 m long, sparse-pilose, especially at base of petioles and peduncles. *Leaves* with small and caducous stipules; petioles 6–8 cm long; the lamina orbicular to somewhat reniform, 3–5 (–6) cm long, 4–7(–9) cm broad, peltate, slightly 5-lobed to almost entire, the middle 3 lobes short-mucronate, the base truncate or subtruncate, the principal nerves 3(–5), the lateral nerves forked. *Flowers* on peduncles often shorter than the petioles, 4–7 cm long; calyx lobes heteromorphic, the lower lobes lanceolate, ±12 mm long, 3–4 broad, the upper lobes almost triangular, 10 mm long, 7–8 mm broad at the base, yellow or yellowish; spur 15–16 mm long, straight, slender, slightly conical at the base, yellow, the filiform tip green or greenish; upper petals cuneate to spathulate to obovate, shortly unguiculate, 4–5 mm long, 3–4 mm broad near the apex, irregularly serrate, yellow, with darker veins and normally with a dark violet spot near the apex, lower petals unguiculate 7–8 mm long, the lamina elliptical, 4–5 mm long, serrate at the apex, yellow. *Fruiting carpels* 5–6 mm long, somewhat elongate, ribbed.

This species has a somewhat disjunct distribution in Costa Rica, Panama, Colombia, and Ecuador; and it is variable in its vast and scattered distribution. The species was described on material cultivated in Europe from seeds originating in Costa Rica. The Panamanian material belongs to this typical form.

CHIRIQUÍ: Valley of upper Río Chiriquí Viejo, *White 70* (MO).

5. **Tropaeolum peregrinum** L., Sp. Pl. 345. 1753.—Fig. 5.

T. aduncum Sm. in Rees, Cyclopedia 38. Trop. nr. 5. 1819.
T. "canariense" hort, nomen ined.

High-climbing annual *vine*, normally glabrous, but pilose forms sometimes found. *Leaves* 3–7-lobed, green or somewhat glaucous especially below, 3–7 cm long, 3.5–8 cm broad, the lobes entire or lobulate, acute or rarely obtuse, sometimes mucronate, lanceolate or obovate; petioles 1–11 cm long. *Flowers* axillary, but often forming pseudo-racemes (rarely branched); peduncles longer than petioles; calyx with lobes of different form, the inferior two lobes broadly lanceolate, obtuse, 4 by 10 mm, the superior three lobes shorter, 4 by 6 mm, subacute, yellowish or greenish like the basal part of the spur; spur short, 8–10 mm long, stout, ending in a dark green or brownish hook; petals yellow, often purple-spotted along the nerves near the base, the superior petals large, 15–20 mm long, 12–17 mm broad, ovovate and long-unguiculate, the blade lobed, the lobes lanceolate, obtuse, not mucronate, the claw recurved or rarely straight with a big acute tooth at the bending, inferior petals almost elaminate, long-clawed, 8–10 mm long, with long purple ciliae. *Fruiting carpels* 10–14 mm long, dark brown or blackish; carpophore short.

A species originating from Peru and commonly cultivated around the world, it often escapes from cultivation.

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FLORA OF PANAMA[1]

BY ROBERT E. WOODSON, JR. AND ROBERT W. SCHERY
AND COLLABORATORS

Part VI

FAMILY 87. ERYTHROXYLACEAE

W. G. D'ARCY[2] AND NOEL SCHANEN[2,3]

Trees or *shrubs*; twigs mostly compressed; sap sometimes colored. *Leaves* alternate-distichous, simple, mostly entire, pinnately veined, often deciduous, ptyxis involute; stipules often conspicuous, appearing immediately distal to the petiole, sometimes appearing without leaves (ramenta). *Inflorescences* sessile or subsessile fascicles subtended by bracts; pedicels articulating at the base, subtended by bracteoles. *Flowers* heterostylous, 5-merous; sepals imbricate or valvate, persistent; petals free, alternate with the sepals, mostly ventrally appendaged; stamens 10, in 2 whorls, the outermost alternate with the petals, the filaments basally fused into a tube, the anthers 2-loculed, small; ovary superior, often truncate, 3-loculed, only one bearing a solitary (?rarely 2), pendulous, epitropous, anatropous ovule, styles 3, fused or free, the stigmas globose or turbinate. *Fruit* a baccate drupe, the endocarp hard, 3-loculed but only one containing a shiny seed; endosperm present or not, sometimes copious.

The family may be recognized by its stipulate, entire leaves and by the flowers which have free, appendaged petals and a 3-loculed ovary surrounded by the filament tube. When present, the longitudinal lines or areoles on the leaf undersides are diagnostic in the Panamanian flora. The flowers are heterostylous; in one form the anthers are held above the free styles on equal filaments, in the other form, the anthers are held below the often connate styles on filaments of two lengths.

The Erythroxylaceae are closely related to the Linaceae, Humiriaceae and Malpighiaceae, and they have been united with these families in the past. Some genera of Linaceae, *e.g. Roucheria, Hebepetalum* and *Pepidobotrys*, are not clearly distinct from the Erythroxylaceae, having many floral characters in common and having alternate-distichous leaves with involute leaf ptyxis which sometimes results in lines or areoles on the developed leaves. In addition to *Erythroxylum* with 200–300 species, *Nectaropetalum* P. Br. (6 species in Africa) and *Aneulophus* Benth. (2 species in Africa) are sometimes considered to be members of the Erythroxylaceae.

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Literature:

Schulz, O. E. Erythroxylaceae. *In* A. Engler, "Das Pflanzenreich." 4(134). 1907.

Payens, J. P. D. W. Erythroxylaceae. *In* C. G. G. J. Van Steenis, "Flora Malesiana." I(5): 543–552. 1958.

1. ERYTHROXYLUM

Erythroxylum P. Br., Civ. Nat. Hist. Jamaica 1: 278. 1756. TYPE: *E. aureolatum* L. (1759, non 1770). "*Erythroxylon*" mult. auct.

Sethia H.B.K., Nov. Gen. Sp. Pl. 5: 175. 1821. TYPE: Based on *Erythroxylum monogynum* Roxb.

Steudelia Spreng., Neue Endeck. 3: 59. 1882. TYPE: *S. brasiliensis* Spr. ? = *E. suberosum* St.-Hil. (1828), fide O. E. Schulz.

Roelana Comm. *ex* DC. nomen nudum in syn. *R. laurifolium* Comm., nomen nudum, cited as basionym for *Erythroxylum laurifolium* DC.

Venelia Comm. *ex* Endl., Gen. 1065. 1840. Nomen nudum. Taken up by O. E. Schulz as *Erythroxylum* sect. *Venelia* Comm. *ex* O. E. Schulz for 5 species of Madagascar. TYPE: *E. hypericifolium* Lam.

Glabrous *trees* or *shrubs*; twigs compressed, usually becoming terete; sap sometimes yellow or reddish, bitter. *Leaves* simple, entire, minute to large, alternate-distichous, deciduous often several times a year, ptyxis involute often leaving lines or a distinctly textured areole on the leaf undersides, venation pinnate, the midvein prominent, often excurrent beneath, the lateral veins mostly numerous, anastomosing irregularly with reticulate minor venation both within and beyond the arc of the lateral veins; petioles basally articulated; stipules mostly fused forming a single structure distal to the petiole with 2 median ribs and in some species with numerous striations, sometimes setose or fimbriate, on new growth or near inflorescences sometimes appearing without a leaf (ramenta) or with the leaf reduced to a minute cylindrical stub. *Inflorescence* mostly fasciculate, appearing as the leaves mature, subtended by bracts which resemble the stipules; the pedicels mostly angled, articulated near the base and accompanied by paired bractlets (prophylls). *Flowers* mostly perfect, sometimes subdioecious, heterostylous with the styles and filaments alternating in length; calyx 5-lobed, sometimes wing-angled, the sepals imbricate or valvate, sometimes to a sharp point, persistent; petals free, deciduous, mostly white, the bottom third demarcated from the upper portion, mostly with 2 more or less fused petaloid appendages arising from the horizontal demarcation, often with a nectary situated between the appendages and petal lamina and median to the line of demarcation; stamens 10, in 2 series, the outermost alternate with the petals, the filaments basally fused into a tube, the innermost sometimes ventral to the truncate or dentate rim of the tube, the outermost arising directly from the tube, the anthers 2-loculed, rotund, basifixed, longitudinally dehiscent; ovary ellipsoid or ovoid, mostly slightly truncate, 3-loculed, only one locule ovule-bearing, this with one (?rarely 2) pendulous, epitropous, anatropous ovule. *Fruit* a small, red, baccate drupe, the endocarp hard; seed shiny, endosperm present or wanting, sometimes copious.

Erythroxylum may be recognized by its dorsally ridged stipules, by its alternate-distichous leaf arrangement and frequent leaf fall, and by its small whitish flowers with 10 basally united stamens and 3 stigmas. The shiny red fruit is sometimes conspicuous.

Erythroxylum is now considered to include 200–300 species throughout the tropics with the greatest number of species in South America. The species are for the most part poorly defined and there would seem to be a considerable redundancy of names in use. Perhaps fewer than half of these refer to distinct species. Panama is no exception to this situation, and some of the elements treated here may best be placed with other species from South America. The treatment of the Panamanian species presented here represents the initial stages of a more wide-ranging study of the genus which was terminated before satisfactory understanding of the variability of the plants could be achieved. In the course of this aborted endeavor, type material of many species was kindly made available by curators of herbaria in both America and Europe for which acknowledgement is gratefully made[4]. Dr. Timothy Plowman and Mr. Charles Sheviak, both of Harvard University, are currently undertaking a large-scale study of the genus employing field observations, cytological, chemical and other methods, and this work may clarify the difficulties encountered with regard to the Panamanian plants.

Erythroxylum coca Lam. and some closely related species native to the uplands of Peru and Bolivia are the source of cocaine. These species are also cultivated for cocaine in other parts of the tropics. A number of species are used locally for various medicinal purposes. Traditional use of the leaves for "coca" involves chewing of the leaves with small quantities of unslaked lime several times a day. Besides an immediate warming sensation, this confers endurance to fatique and hunger for long periods. The refined drug cocaine was formerly used for local anaesthesia and for a number of other medical conditions as well as for enjoyment. It acts as a strong nervous stimulant. Public use of the drug was banned by most governments in the early part of this century. Cocaine may be an addictive drug. Medical requirements for cocaine have been largely supplanted by novocain and other drugs lacking undesireable features of cocaine.

a. Stipules and bracts longitudinally many-striate, sometimes more than 5 mm long; leaf undersides without a pair of distinct lines longitudinally flanking the midvein.
  b. Leaves broad, mostly more than 10 cm long; petiole more than 1 cm long; flowering branch with numerous empty large bracts or stipules (ramenta) below the lowest fascicle; flowers in dense clusters surrounding and obscuring the stem; pedicels 8–20 mm long; fruiting calyces more than 4 mm long ..... 1. *E. multiflorum*

bb. Plants not as above, leaves mostly much smaller, often narrow; petioles less than 1 cm long; bracts or ramenta less than 1.5 cm long and not clustered below the fascicles; flowers solitary or in discrete clusters (fascicles); pedicels mostly less than 8 mm long; fruiting calyces less than 3 mm long.
  c. Leaves rigidly coriaceous, broadly elliptical, less than 8 cm long, more than half as broad as long ..... 2. *E. campestre*

[4] In particular, large amounts of material were lent by curators at A, BM, DUKE, F, GOETT, GH, K, P, S, US.

cc. Leaves membranaceous or if coriaceous then less than half as broad as long and more than 8 cm long.
d. Flowers accompanied by bracts or stipules more than 3 mm long; sepals ovate with conspicuous, lighter colored margins, mostly more than 1.5 mm long, slightly imbricate in bud.
e. Sepals more than 1.5 mm long, ovate; leaves mostly more than 10 cm long, more than 4.5 cm wide; stipules various ---------- 3a. *E. lucidum* var. *lucidum*
ee. Sepals less than 1.5 mm long, deltoid; leaves mostly less than 10 cm long; stipules less than 11 mm long ---------- 3b. *E. lucidum* var. *costaricense*
dd. Flowers not accompanied by bracts or stipules (stipules mostly deciduous before flowers develop); sepals acute with thin, inconspicuous margins, less than 1.5 mm long, not imbricate in bud ---------- 4. *E. citrifolium* var. *minus*

aa. Stipules and bracts with two dorsal ridges but not striate, not more than 5 mm long; leaf undersides sometimes with a pair of lines longitudinally flanking the midvein.
f. Leaves narrow, more than 2.5 times as long as broad, acute at both ends, mostly more than 4 cm long.
g. Lines on leaf undersides flanking the midvein indistinct, interrupted or wanting; pedicels with distinct, rounded angles; sepals deltoid, divided halfway down, not striate ---------- 5. *E. panamense*
gg. Lines on leaf undersides flanking the midvein prominent, continuous; pedicel angles not well demarcated; sepals acute, divided more than halfway down, drying minutely striate ---------- 6. *E. davidii*
ff. Leaves broad, less than 2.5 times as long as broad, apically obtuse, rounded, or emarginate, not acute, mostly less than 6 cm long.
h. Lines on leaf undersides flanking the midvein prominent; leaves broadly elliptical, obtuse at each end; pedicels about as long as the calyx, strongly thickened upwards ---------- 7. *E. brennae*
hh. Lines on undersides flanking the midvein wanting or rare; leaves obovate or spathulate, the base narrower than the apex; pedicels about 1½ times as long as the calyx, little thickened upwards ---------- 8. *E. havanense*

1. **Erythroxylum multiflorum** Lundell, Amer. Midl. Naturalist 29: 474. 1943. TYPE: Panama, *Bartlett & Lasser 16566* (MICH, holotype, not seen; MO, DUKE, isotypes).—FIG. 1A, E, F, H.

Glabrous *tree* to 10 m tall; bark greenish gray, light colored, smooth or minutely striate; twigs stout, slightly compressed but soon terete and sometimes prominently ringed with stipule (ramenta) scars. *Leaves* alternate-distichous, large, to 40 cm long, coriaceous, elliptical, apically short acuminate into a weakly developed drip-tip, basally obtuse, the margins subrevolute, the midvein stout, especially prominent in the lower half, the lateral veins 12–22 on each side, the minor reticulation obscure or evident, longitudinal lines wanting and the areole area quite indistinct; petioles drying dark, stout, ca. 15 mm long, basally articulated, the minute wings upfolded to form a ventral trough; stipules conspicuous, drying reddish brown, to 7 cm long and 8 mm wide basally, encompassing about ½ the circumference of the stem, the costa of 2 sharp ridges, the surface prominently many-striate, sometimes subtending a minute, peg-like, rudimentary leaf. *Inflorescence* a cluster of fascicles near the ends of the branches, appearing as the leaves mature but before the next flush of leaves is apparent, the flower cluster dense, to 5 cm long and sometimes forming a cylinder (spike) 3.5 mm in diameter which completely surrounds and occludes the stem; bracts and the paired bracteoles similar to the stipules in color and ornamentation; pedicels

FIGURE 1. *Erythroxylum*—A. Fruiting branch (× ⅓), *E. multiflorum* Lundell.—B. Twig with emerging leaves and expanded leaf underside (× ⅔), *E. brennae* D'Arcy & Schanen. —C–D. Stipules (ramenta) (× 3⅓).—C. *E. citrifolium* var. *minus* O. E. Schulz.—D. *E. panamense* Turcz.—E. Gynoecium with surrounding androecium (× 2⅔), *E. multiflorum*. —F. Ventral view of petal with appendages (× 3⅓), *E. multiflorum*.—G–K. Flowering calyces.—G. *E. brennae* (× 3⅓).—H. *E. multiflorum* (× 2⅔).—I. *E. lucidum* H.B.K. var. *lucidum* (× 2⅓).—J. *E. davidii* D'Arcy & Schanen (× 3⅓).—K. *E. panamense* Turcz. (× 3⅓). [A, E, F, H after *Lao & Holdridge 226* (MO). B after *Gentry et al. 3450* (MO). C after *Lewis et al. 254* (MO). D, K after *Croat 5579* (MO). G after *Tyson 3385-A* (SCZ). I after *Wedel 2405* (MO). J after *Kirkbride & Duke 1284* (MO).]

7–9 mm long, becoming 10–20 mm long in fruit, prominently angled, almost alate, articulated just above the base. *Flowers* 5–6 mm across, heterostylous; the calyx ca. 6 mm long, leathery, the sepals apically acute, dorsally darkened with a thick costa, the connate angles forming a ridge which continues from the angles of the pedicel; petals white, free, ca. 6 mm long, carinate, the costa a reddish reticulum, the dorsal appendage about ½ as large as the petal, a nectary median on the petal lamina on the distal side of the appendage junction; stamens 10, basally united into a persistent tube surrounding the ovary, the filaments 3–4 mm long, the anthers small, reddish, ellipsoidal; ovary weakly trilobate, the styles free, 1.5 mm long, outward-curving, the stigmas capitate. *Fruit* a red, juicy, obturbinate drupe 8–10 mm long, subtended by the persistent calyx and filaments and surmounted by the persistent styles.

This species is best recognized in the Panamanian flora by its large leaves and conspicuous clusters of narrow, reddish stipules (ramenta). The cylindrical, dense, many-flowered inflorescence with relatively large flowers distinguish it from other species of *Erythroxylum*.

Erythroxylum multiflorum belongs to a wide-ranging group of New World species which differ in details which alter the gross appearance of the plants but may be of little taxonomic importance. *Erythroxylum macrocalyx* Cav. is the earliest name for species in this group. It refers to plants from Brasil and eastern South America which differ in having less conspicuous stipules which are not clustered below the inflorescences (sometimes above it), smaller inflorescences, and slightly smaller flowers. Included in this group also are *E. amplum* Benth., *E. floribundum* Mart., *E. tabascense* Britt., all earlier names than *E. multiflorum* but differing mainly in vegetative characters.

This species is found in lowland central Panama. Most collections have been taken on Barro Colorado Island, perhaps reflecting collecting activity rather than abundance.

CANAL ZONE: Hill at Canal Zone boundary near Juan Mina, *Bartlett & Lasser 16566* (DUKE, MO). Road on Río Piña-Río Media divide, *Johnston 1811* (A, MO). Barro Colorado Island, *Aviles 47* (F); *Bailey & Bailey 399* (F); *Bangham 397* (A, F); *Croat 6539, 8265, 12679* (all MO); *Ebinger 584* (GH, MO); *Foster 1189* (F, DUKE, MO), *1331* (DUKE, MO); *Kenoyer 454* (US); *Knight 9* (F); *Salvoza 866* (A); *Shattuck 1022* (F, MO, US); *Standley 40873* (US). COLÓN: Santa Rita lumber road, *Correa & Dressler 770* (MO). Salud, *Lao & Holdridge 226* (MO). Wooded swamp between France Field and Catival, *Standley 30218* (US).

2. **Erythroxylum campestre** St.-Hil., Fl. Bras. Merid. 2: 70. 1829. TYPE: Brasil, *Saint-Hilaire* (not seen).

Shrub, to 3 m tall; twigs somewhat compressed, stout, soon becoming terete; bark smooth. *Leaves* appearing on short shoots ca. 6 cm long, broadly elliptical, to 6 cm long and 4 cm wide, apically minutely emarginate and mucronulate, basally obtuse, stiffly coriaceous, the midvein prominent, excurrent beneath for the proximal third, the lateral veins ca. 7 on each side, prominent beneath, obscure above; stipules to 4 mm long, striate, soon deciduous. *Inflorescences* few-flowered; pedicels (in fruit) 5 mm long with distinct rounded angles; bracts and bractlets inconspicuous. *Flowers* (fide Schulz) with the calyx lobed ¾ way

down, the sepals 1.5 mm long, deltoid, keeled; petals 4 mm long, ventrally appendaged; stamens 3.5 mm long. *Fruit* red, 7–10 mm long, variable in diameter.

This species is distinct from other Panamanian species in its very firm, broadly rotund, small leaves which have relatively few but conspicuous lateral veins. *Erythroxylum campestre* was considered by Schulz to occur only in southern Brasil, but more recent collections from the Guyanas appear to extend this range. In a bird-dispersed group of plants such as this, it is not surprising to find widely disjunct populations outside the established range of a species. The Panamanian collection bears a number of aborted fruits with the pedicel and ovary persistent, suggesting some reproductive difficulties.

PANAMÁ: Cerro Jefe, summit to 1 mi. beyond, 3100 ft, *Gentry et al* 3537 (MO, PMA).

3. **Erythroxylum lucidum** H.B.K., Nov. Gen. Sp. Pl. 5: 179. 1821. TYPE: Colombia, *Humboldt & Bonpland* (P; F, fragment).

3a. **Erythroxylum lucidum** H.B.K. var. **lucidum**.—FIG. 11.

Shrub or *tree* to 5 m tall; twigs drying reddish brown, furrowed, slightly compressed, becoming terete after fall of first leaves. *Leaves* mostly elliptical, 10–15 cm long, apically short acuminate, mucronulate, basally rounded or obtuse, the margins mostly not revolute or only slightly so, subcoriaceous, the midvein prominent beneath in the lower half, the lateral veins 10–18, the minor venation reticulate, sometimes more pronounced in a central, aureole area; petioles 5–8 mm long, sometimes stout; stipules conspicuous on new growth, often soon-deciduous, 1–2 cm long, conspicuously striate, reddish brown. *Inflorescence* mostly a several-flowered fascicle subtended by a stipule-like bract, the paired bracteoles 2–3 mm long; pedicels strongly angled or alate, articulated just above the base. *Flowers* with the sepals ovate, 1.5–4 mm long, imbricate in bud, the sutures often expanded into wings running from the pedicel angles; petals white, about twice as long as the sepals, ventrally appendaged; filament tube slightly shorter than the ovary; ovary truncate, slightly 3-lobate, the stigmas slightly oblique. *Fruit* red, juicy, 5–10 mm long, ovoid, the costa of the persistent calyx drying dark.

This variety is intermediate between *E. multiflorum* and *E. lucidum* var. *costaricense* in leaf, stipule and flower size, and some Panamanian collections are difficult to separate. *Erythroxylum lucidum* ranges from Brasil to Costa Rica, and is cultivated in India for ornament and local medicinal purposes. The name refers to the shiny, slate-hued leaf upper-sides which contrast with the frequently reddish leaf undersides. It is reported to be a useful ornamental subject.

Three collections cited below (*Gentry 2801*; *Wedel 424, 2405*) may represent a distinct species. They have more slender stipules, and the calyx is more deeply dissected into acute lobes in comparison with other material seen of *E. lucidum*. In Schulz's treatment these key out to *E. macrocnemium* Mart. from Brasil, but the one syntype seen of that species, *Poeppig 2166* (P), has much larger leaves, pedicels, and flowers than the Panamanian collections. As none

of the Panamanian collections is adequate for satisfactory determination, they are placed under *E. lucidum* which they closely resemble.

BOCAS DEL TORO: Cricamola, *Cooper 494* (F, NY). Above Almirante, *Gentry 2801* (MO). Without locality, *Wedel 424* (US). Fish Creek Hills, *Wedel 2405* (GH, MO, US). CHIRIQUÍ: San Lorenzo, *Seemann 1624* (BM). Around Caldera, 200–300 m, *Pittier 3354* (US). COLÓN: Zona maderera de Santa Rita, *Correa & Dressler 770* (DUKE). Without locality, *Duke 15288* (MO). Santa Rita Ridge 19 km from main highway, *Dwyer 8567* (MO). DARIÉN: Cerro Pirre, *Bristan 570* (MO). LOS SANTOS: Bahia Honda near Puebla Nueva, *Barclay 2822* (MO). HERRERA: 12.5 mi. S of Ocú, 1200 ft, *Lewis et al. 1655* (MO). PANAMÁ: Cerro Campana ¾ way to summit from Panamerican Highway, *Dwyer et al. 4712* (MO). Trail into forest 4.8 mi. N of Panamerican highway just W of El Llano, *Gentry 5079* (MO). Near San Blas border 5–6 mi. N of El Llano, 1300 ft, *Gentry 5815* (MO). Cerro Campana, *Porter et al. 4304* (MO). VERAGUAS: Trail between Cañazas and foot of Cordillera Central, headwaters of Río Cañazas, 300–600 m, *Allen 162* (A, F, MO). Isla de Coibe, *Dwyer 2321* (MO). Isla de Coibe, *Mendez 145* (US). Between San Francisco and Santa Fé, *Stern et al. 1921* (US).

3b. **Erythroxylum lucidum** var. **costaricense** (Donn. Sm.) O. E. Schulz *in* Engler, Pflanzenr. 4 (134): 25. 1907.

E. costaricense Donn. Sm., Bot. Gaz. (Crawfordsville) 13: 240. 1897. TYPE: Costa Rica, *Tonduz 10092* (CR, holotype, not seen; BM, US, isotypes; NY, fragment).

Shrub or small *tree* to 4 m tall; twigs flat, not becoming terete for several seasons. *Leaves* elliptical, apically acute or obtuse, mucronulate, basally obtuse, the margins minutely revolute, coriaceous, the midvein prominent, the minor venation mostly inconspicuous but in some specimens manifestly dark-reticulate in the underside, the upper surface shiny, often slate-colored, dull and reddish brown beneath; stipules, ca. 7 mm long, striate, deciduous or not. *Inflorescence* a series of several-flowered fascicles axillary to and amongst the mature leaves; bracts ca. 10 mm long resembling the stipules but slightly larger; pedicels ca. 3 mm long, stout or slender, sharply angled. *Flowers* small; the calyx 1.5–2 mm long, divided more than halfway down, the sepals 1–1.5 mm long, ovate, the costa sometimes carinate or conspicuous; petals white, about twice as long as the sepals with a prominent costa; the filament tube shorter than the ovary, much shorter than the sepals; ovary truncate, the styles connate or not, stigmas capitate. *Drupe* red, baccate, 7–8 mm long, ellipsoidal or ovoid.

This variety differs from the typical in its small calyx and small leaves. Considered only against the Panamanian taxa, this would probably merit recognition at the species level, but when the wide range of variation in var. *lucidum* from South America is considered, the differences of *E. costaricense* lose some significance and argue for recognition as a variety of the widepread species.

Most collections of this variety are from El Valle or Cerro Campana, hills just west of the Canal Zone.

CHIRIQUÍ: Boquete, 3800 ft, *Davidson 629* (A, F, MO, US). Coppiced dwarf forest near Pinola dominated by *Vismia*, *Rondeletia* and various melastomes, *Kirkbride & Duke 869* (MO). Finca Lerida to Boquete, 1300–1700 m, *Woodson et al. 1105* (A, F, MO, NY). COCLÉ: South (dry) rim of El Valle, 600–1000 m, *Allen 1772* (GH). North (wet) rim of El Valle, 600–1000 m, *Allen 1802* (F, GH, NY, US). Between Las Margaritas and El Valle, *Woodson et al. 1305* (A, F, NY). Bismark above Penonomé, *Williams 543* (NY). PANAMÁ: Dry slopes of Campana Hill, ca. 600 m, *Allen 2447* (NY). Edge of forest, Cerro Campana, 2800 ft, *McDaniel 6835* (MO).

4. **Erythroxylum citrifolium**[5] var. **minus** O. E. Schulz *in* Engl., Pflanzenr. 4(134): 37. 1907. TYPE: Not designated; syntype, Brasil, *Riedel* 386 (MO). —FIG. 1C.

Shrub or *tree* to 7 (13) m tall; twigs compressed but soon terete, drying dark. *Leaves* narrowly elliptical, 17–24 cm long, to 3.5 cm wide, apically acuminate, mucronulate, basally obtuse or rounded, the margins often subrevolute, the midvein drying reddish brown, prominent, the minor venation inconspicuous except near the midvein in the areole area, longitudinal lines flanking the midrib wanting or quite obscure, coriaceous, drying darker and almost shiny above; petioles 3–5 mm long, drying dark; stipules striate, 3–5 mm long, the costa sometimes apically excurrent, mostly deciduous before leaf maturity. *Inflorescences* few- to several-flowered fascicles, mostly maturing after leaf fall and thus appearing discrete along the stems; pedicels 4–6 mm long, compressed or 5-angled, the angles weak or distinct, articulated near the base. *Flowers* with the calyces ovate, not prominently margined, ca. 1 mm long, divided halfway or a little more; petals white, 2–3 mm long, ventrally appendaged; filament tube slightly shorter than the ovary; styles mostly not connate, ovary truncate. *Fruit* red, juicy, ovoid, 7–9 mm long.

Specimens of this species closely resemble those of *E. panamense* and *E. lucidum* var. *costaricense* in the appearance of the leaves, but the stipules, ornamentation, calyx size and the usual absence of stipules from flowering areas are noticeable distinctions. *Erythroxylum citrifolium* ranges from Mexico to Colombia and perhaps Peru. Variety *minus* is known from southern Brasil and the Guyanas, and in Panama it is known only from Cerro Jefe, a range of hills ca. 20 mi. northeast of Panama City.

CANAL ZONE: Advanced secondary forest between Fort Sherman and Fort San Lorenzo, *Croat 15432* (MO). COLÓN: Achiote, *Tyson et al. 4548* (MO). PANAMÁ: Río Charco-Espiritu on Tocumen Highway, *Duke 5742* (MO). Cerro Azul, *Dwyer 1387* (MO), *1529* (MO, NY, US), *1897* (US), *2191* (GH, MO), *2790* (MO); *Ebinger 425* (GH, MO, US), *990* (MO, US). 2–3 mi. S of Goofy Lake, road to Cerro Jefe, 2000–2200 ft, *Lewis et al. 254* (MO, DUKE, NY). Cerro Azul, 2000 ft, *Tyson 2145* (MO). Between Cerro Azul and Cerro Jefe, *Tyson et al. 4316* (MO).

5. **Erythroxylum panamense** Turcz., Bull. Soc. Naturalistes Moscou 36(1): 581. 1863. TYPE: Panama, *Fendler 193* (BM, F, GH, K, MO, NY, US).—FIG. 1D, K.

Shrub or *tree* to 4 m tall; twigs flat, soon terete, the branches with numerous lenticels. *Leaves* alternate-distichous, appearing terminally and on short shoots, mostly elliptical, sometimes narrow, to 9 cm long, apically obtuse, acute or acuminate, mucronulate, basally obtuse, the margins seldom subrevolute, chartaceous, the midvein prominent, reddish, especially in the lower half, the minor venation mostly obscure, an areole often present represented by two distinct but irregular

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[5] *E. citrifolium* St.-Hil., Fl. Bras. Merid. 2: 67. 1829. TYPE: Goyas, Brasil, *Saint-Hilaire* 755 (P). The type collection of *E. citrifolium* has much larger, broader, and more coriaceous leaves than the Panamanian material considered here and is a close match for what Schulz considered as var. *latifolium*.

lines or merely by an area of distinct texture; petioles ca. 3 mm long, canaliculate; stipules bicostate, otherwise not striate, 2–3 mm long, sometimes minutely ciliate or scarious margined, often persistent. *Inflorescences* numerous, almost crowded, several-flowered fascicles; bracts resembling the stipules; pedicels 1–2 mm long with well marked, rounded angles. *Flowers* numerous, fragrant, with the calyx ca. 1 mm long, divided about halfway, the lobes deltoid, valvate in bud; petals white, 3–4 mm long, the broad, thick costa drying reddish brown, ventrally appendaged, with a nectary between the appendage and the petal lamina; filament tube as long as or slightly shorter than the ovary; ovary mostly truncate, the stigmas capitate. *Fruit* a juicy red drupe 7–9 mm long, ellipsoid, slightly curved.

This species may be recognized by its chartaceous, narrow leaves which often have lines marking an areole on the leaf undersides. The minute persistent stipules and usually numerous flowers are also useful for identification.

Erythroxylum panamense is endemic to lowland Panama. It blooms at intervals throughout the year.

CANAL ZONE: Near Río Providencia 12 mi. S of Colón, *Blum & Tyson 2330* (MO). Pipeline Road at Río Agua Salud, *Croat 4741* (MO, DUKE, NY). Coco Solo, U.S. Army Tropic Test Center, Mine Emplacement Center, *Dwyer & Dyke 7871* (MO). Fort Gulick, *Dwyer & Robyns 166* (MO, US). Río Congo, open woods, W of Limón Bay, Gatun Locks and Gatun Lake, *Johnston 1759* (A, MO). Damp woods at Bohio Station, Panama Railroad, *Hayes 145* (BM, MO). Forests on dry limestone around Alhajuela, Chagres Valley, *Pittier 3475* (GH, NY, US). Barro Colorado Island, *Aviles 74* (F, MO); *Bailey & Bailey 392* (F); *Bangham 598* (A, F); *Croat 4879* (MO), *5168* (F, MO), *5519* (F, MO), *5579* (MO), *5703* (MO), *6596* (MO, NY), *7743* (MO), *7764* (MO), *8537* (DUKE, MO, NY), *8662* (MO), *8693* (MO), *11127* (MO), *15588* (MO); *Ebinger 616* (F, MO, US); *Foster 287, 625, 749* (all DUKE); *Knight 69–2* (MO); *Salvoza 988* (A); *Shattuck 858* (F, MO, US); *Standley 41008, 41051* (both A, US); *Wilson 133* (F); *Woodsworth & Vestal 424, 528* (both A, F, MO). COLÓN: Lowland rain forest ca. 3 mi. up Río Guanche, *Kennedy & Foster 2167* (MO). DARIÉN: Near Río Uruti, *Bristan 212* (MO). Cerro Pirre, *Bristan & Duke 1229A* (MO). Above Pucro along Quebrada Maskia off Río Pucro, *Duke 13092* (MO). Punto Sabanas opposite La Palma, Golfo de San Miguel, *Gentry 3955* (MO). LOS SANTOS: Loma Prieta, 800–900 m, *Duke 11882* (MO). Valle Punta Blanca, W of Tonosí, *Holdridge 6230* (MO). PANAMÁ: Ceremeño, *Dwyer 5605* (MO). Sabanas N of Panama City, *Paul 608* (US). Isla Espiritu Santo, Pearl Islands, *Tyson 5566* (DUKE, MO). SAN BLAS: Permé, *Cooper 236* (F, GH, NY, US). Río Cuadi ca. 6 air mi. SW of Mulatupu, 100 m, *Duke 14215* (MO). VERAGUAS: Above Santa Fé on slopes of Cerro Tuté below Agricultural School, *Gentry 6230* (MO).

6. **Erythroxylum davidii** D'Arcy & Schanen[6]. TYPE: Panama, *Kirkbride & Duke 1284* (MO, holotype).—FIG. 1J.

Tree or *shrub* to 4 m tall; twigs flat, drying striate, reddish brown, soon terete and displaying numerous lenticels. *Leaves* elliptic, to 15 cm long, mostly narrow, apically short acuminate or acute, basally acute or obtuse, chartaceous, the margins not revolute, the midvein prominent beneath, flanked by two prominent, continuous lines on the undersides, the minor venation obscure except between the longitudinal lines; petioles ca. 3 mm long, slender, drying reddish brown; stipules minute, 1 mm long, chartaceous-scarious, sometimes deciduous, often associated with rudamentary leaves. *Inflorescences* scattered, few-flowered

[6] *Erythroxylum davidii* sp. nov. Species *Erythroxylum brennae* D'Arcy & Schanen simile, differt foliis maioris, tenuioribus, sepalis minoribus, antheris longioribus, appendicibus petalorum minoribus. Nomen Davidii Schaneni designatur ad hunc *Erythroxylum*.

fascicles; bracts and bracteoles minute; pedicles 3–4 mm long, compressed, the angles not distinct. *Flowers* small; calyx 1–1.5 mm long, divided deeply, the sepals acute, thick, minutely striate, the margins not demarcated; petals white, 4 mm long, the upper portion dorsally overlapping the lower portion, and the 2 portions marked about ¼ the way up, the ventral appendages not rising more than half the length of the whole petal; stamens about equalling the sepals, the anthers oblong. *Fruit* red, juicy, ellipsoidal, ca. 8 mm long.

This species may be recognized by its chartaceous or membranaceous leaves with conspicuous longitudinal lines on the undersides. The anthers are proportionally longer than other species in Panama and the upper portion of the petal exceeds the lower portion and the appendages by a relatively greater length than other species. The calyx is quite similar but slightly smaller than that of *E. brennae*. *Erythroxylum davidii* is known only from the vicinity of Cerro Pirre, a low mountain in east-central Darién. This is some 250 km distance from Cerro Jefe, the locality where *E. brennae* is known.

DARIÉN: Cloud and mossy forest, Cana trail between Cerro Campamiento, La Escalera to "paramo" E of Tres Bocas, *Kirkbride & Duke 1284* (MO).

7. **Erythroxylum brennae** D'Arcy & Schanen[7]. TYPE: Panama, *Correa & Dressler 703* (MO, holotype; DUKE, isotype).—FIG. 1B,G.

Much branched *shrub* to 4 m tall; twigs drying dark with conspicuous whitish lenticels, compressed but soon terete. *Leaves* uniformly elliptical, broad, mostly obtuse at each end, to ca. 4 cm long and 3 cm wide, mucronate, the margins slightly revolute, the midvein prominent beneath drying reddish brown, the minor venation mostly obscure but sometimes somewhat more prominent above, 2 conspicuous longitudinal lines regularly flanking the midvein beneath, coriaceous, drying dark grey-green above and sometimes shiny, dull, reddish or chocolate brown beneath; petioles 1–3 mm long, drying dark; stipules bicostate but otherwise not striate, 1.2 mm long, deciduous or not, the narrow margin scarious. *Inflorescence* 1- to few-flowered; bracts and bractlets minute, scarious margined; pedicels 2–3 mm long, drying dark, the angles contrasting. *Flowers* small, the calyx ca. 2.5 mm long, divided halfway into acute sepals, fleshy, minutely striate, the margin not demarcated; petals white, 3.5 mm long, the lamina creased about ⅓ the way to the apex, the ventral appendages about ½ as long as the upper portion, nectary not evident, the tube 1 mm long, as long as or slightly shorter than the ovary; filaments ca. 2 mm long; ovary ca. 1 mm long, ellipsoid, apically sinuate-truncate with 3 longitudinal sutures, the styles connate, free in the apical portion, the stigmas disciform, situated laterally at the style apex. *Fruit* a narrowly ellipsoid, red, juicy drupe 10 mm long, deeply sulcate on drying.

This species is known only from Cerro Jefe, a range of hills ca. 25 km NE of Panama City. It is distinctive in its uniformly small, coriaceous, broadly ellip-

[7] *Erythroxylum brennae* D'Arcy & Schanen, sp. nov. Species *E. davidii* D'Arcy & Schanen simile, differt lineis dorsualibus foliorum validioribus, stipulis, foliisque minoribus, inconspicuibus, sepalis acutis, minute striatis, non marginatis, foliis coriaceis. Nomen Brennae Schanenae designatur ad hunc *Erythroxylum*.

tical leaves which bear conspicuous brownish lines on each side of the midvein beneath and faintly evident from above. It is somewhat similar to material from the Bahamas going under the name *E. obovatum* Macf.

PANAMÁ: Cerro Azul 3 mi. before Goofy Lake, *Correa & Dressler 703* (DUKE, MO). Along road from Cerro Jefe toward La Eneida, *Croat 13089* (MO). Goofy Lake to 8 mi. S toward Cerro Jefe, *Dwyer 7086* (MO). Cerro Jefe, *Dwyer 8502* (MO). Cerro Jefe 3 mi. beyond Finca del Indio, *Gentry 2135* (MO). Near top of Cerro Jefe, *Gentry et al.* 3450 (MO). E. slope of Cerro Jefe, in "Clusia" forest, 2700 ft, *Tyson 3385-A* (GH, SCZ).

8. **Erythroxylum havanense** Jacq., Enum. Pl. Carib. 21. 1760; Hist. Stirp. Amer. 135, *t. 87, fig. 2.* 1763. TYPE: Cuba, *?Jacquin* (not seen).

E. ovatum Cav., Diss. 8: 404. 1789, *t.* 233. TYPE: (not seen).
E. cumanense H.B.K., Nov. Gen. Sp. Pl. 5: 137. 1821. LECTOTYPE: Colombia, Magdalena, Villa Vieja, *Humboldt & Bonpland* (P).
E. hondense H.B.K., Nov. Gen. Sp. Pl. 5: 136. 1821. TYPE: Colombia, *Humboldt & Bonpland* (?P, not seen; MO, photo).
E. mexicanum H.B.K., Nov. Gen. Sp. Pl. 5: 137. 1821. LECTOTYPE: Mexico, Chilpancingo, *Humboldt & Bonpland* (P; F, fragment).
E. pringlei Rose, Contr. U. S. Natl. Herb. 8: 314. 1905. TYPE: Mexico, *Pringle 840* (GOETT).

Shrub to 5 m tall; twigs reddish brown, soon terete and greyish, lenticels prominent on newly emerged growth. *Leaves* often on short shoots, elliptic, obovate or spathulate, mostly broadest above the middle, apically obtuse, rounded or emarginate, basally acute or obtuse, the margins sometimes subrevolute, the midvein prominent beneath, the minor venation reticulate, mostly not conspicuous, coriaceous to chartaceous, mostly firm, sometimes shiny above; petioles short, 1–3 mm long, slender; stipules bicostate but otherwise not striate, persistent. *Inflorescences* often on short shoots, several slowered; the bracts small, inconspicuous; pedicels 4–6 mm long, striate but not especially angled. *Flowers* with the calyx divided about halfway down into deltoid, 1-mm-long sepals, the costa evidently continuous from the upper portion of the pedicel; petals (ex Schulz) white, 4.5–5 mm long, ventrally appendaged; filament tube slightly shorter than the sepals, about as long as the ovary; styles somewhat expanded. *Fruit* a red, juicy drupe, ellipsoid, ca. 8 mm long, drying sulcate.

This species may be recognized by its small blunt leaves which often appear on short shoots off the main stem. The inflorescences too are often on short shoots. In Panama and in some other countries *Erythroxylum havanense* occurs mainly near the sea in thickets, but there are several collections from inland stations.

Erythroxylum havanense is a wide ranging species, although it is known under a number of different names in different countries. A number of synonyms from South America appear to be conspecific with this concept.

CANAL ZONE: Coast between Farfan Beach and Vera Cruz, *Duke 11736* (MO). Near beach at Fort Kobbe, *Gentry 6437* (MO). Las Cascades Plantation, near Summit, *Standley 25698* (MO). PANAMÁ: Low woods E of Bella Vista, a suburb of Panama City, *Maxon & Valentine 6954* (GH, NY, US). Alrededores de la entrada de Chamé, *Morón 19* (MO). Coastal thicket, Bella Vista, *Standley 25355* (US). Near Punta Paitilla, *Standley 26251* (US). Nuevo San Francisco, *Standley 30775* (US).

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FLORA OF PANAMA[1]

BY ROBERT E. WOODSON, JR. AND ROBERT W. SCHERY
AND COLLABORATORS

Part VI

FAMILY 87A. HUMIRIACEAE

ALWYN H. GENTRY[2]

Trees. Leaves alternate, simple, more or less coriaceous, entire or serrate, often glandular punctate near margin on underside, stipules small, deciduous or lacking. *Inflorescence* axillary or terminal, paniculate. *Flowers* perfect, actinomorphic; the sepals 5, persistent, thick at base and thinner toward margin, more or less connate into a tube or cupule; petals 5, often deciduous, free, white, greenish, or yellowish white, rarely red; estivation cochlear or quincuncial; stamens numerous or 10–30 and 1–2 seriate, the filaments of alternating lengths, connate at the base, the anthers with 2 bilocular, longitudinally dehiscing thecae or with 4 or 2 unilocular thecae dehiscing by detachment, the connective thick, usually produced as an apiculate or linguiform appendage, staminodia occasionally present, these resembling the filaments but smaller; pollen grains 3-colporate or 4-colporate; disc free, intrastaminal, cupular and surrounding the ovary, dentate, laciniate, or composed of 10–20 free scales; pistil 5-carpellate (rarely with 4, 6, or 7 carpels), the ovary ovoid or ellipsoid, sessile, with axile placentation, each locule 1 or 2 ovulate, the style erect, usually as long as the stamens or shorter, the stigma more or less capitate, usually 5-lobate, the ovules anatropous. *Fruit* drupaceous, often large, the exocarp pulpy to fibrous, coriaceous, endocarp woody, usually very hard, with many resin-filled, round cavities, rarely spongy woody, (4–) 5 (–7)-septate, usually with only 1–2 seeds developed, with as many longitudinal opercula or valves as carpels, often with subapical foramina; seeds oblong, often adherent to endocarp, the embryo straight or slightly curved, the cotyledons oblong or ovate, often subcordate at base, the endosperm fleshy and oily.

A tropical family with 8 genera and 50 species in the neotropics and a single disjunct species of *Sacoglottis* along the West African coast. Species of the family are important constituents of the neotropical rain forest and are occasionally also found in savanna or caatinga formations. A number of fossils are known. The wood of this family is hard and locally used in construction. The bark and wood of some species of *Humiria* produce the "umiry-balsam" or "umiri" of commerce, and the exocarp of the fruits of some species is edible. The exo-

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[1] Assisted by National Science Foundation Grant GB-36202X (Thomas B. Croat, principal investigator).

[2] Missouri Botanical Garden, 2315 Tower Grove Avenue, St. Louis, Missouri 63110.

ANN. MISSOURI BOT. GARD. 62: 35–44. 1975.

carp and seeds of many species are rich in a fatty oil which is sometimes used in the domestic economy of Amazonia.

In Panama all species of Humiriaceae are large (often to 30 or 40 m) forest trees which occur only in well-drained areas below 500 meters altitude. All Panamanian collections of the family have been made since 1970. Despite the paucity of collections, some species of this family are rather common and may be the most dominant element of lowland wet forest in parts of Panama. The Panamanian species can usually be recognized in the field by an unbranched trunk with rather smooth, often minutely-flaky, dark-reddish-drying outer bark, red inner bark, and a dense rounded crown with dark green leaves. The endocarps of fallen fruits may be present on the ground for a year or more and often cover the ground beneath large trees. Members of this family are restricted to the Holdridge system tropical wet forest and premontane wet forest life zones in Panama and may be used as indicator species for these life zones.

Literature:

Cuatrecasas, J. A taxonomic revision of the Humiriaceae. Contr. U. S. Natl. Herb. 35: 24–214. 1961.[3]

a. Stamens 50–180; anthers with 2 bilocular thecae; endocarp with 5 separated lingulate valves extending most of its length ..... 3. *Vantanea*

aa. Stamens 10–30; anthers with 2 unilocular, free thecae; endocarp with the valves broad and adjacent or short and opercular.

b. Stamens 10; anther thecae inferolateral; endocarp inconspicuously grooved, not foraminate at apex ..... 2. *Sacoglottis*

bb. Stamens 20; anther thecae basal; endocarp conspicuously 5-foraminate at apex ..... 1. *Humiriastrum*

1. HUMIRIASTRUM

Humiriastrum (Urb.) Cuatr., Contr. U. S. Natl. Herb. 35: 122. 1961.

Saccoglottis subgen. *Humiriastrum* Urb. *in* Mart., Fl. Bras. 12(2): 443. 1877. TYPE: *H. cuspidatum* (Benth.) Cuatr.

Trees. *Leaves* coriaceous or subcoriaceous, entire or dentate. *Inflorescence* axillary or pseudoterminal, paniculate, mostly with trichotomous or dichotomous branching, the bracts persistent or deciduous. *Flowers* with sepals suborbicular, imbricate, united at base; petals free, thick-membranaceous, linear or oblong; stamens 20, in 2 alternating lengths, glabrous, the anthers ovate-lanceolate or oblong, attached near base, the thecae 2, unilocular, basal, the connective thick, acute at apex; disc a dentate ring or composed of more or less free scales; carpels opposite sepals, ovary 5-locular, the cells uniovulate, the style short, the stigma capitate-lobate. *Fruit* a medium-sized or small drupe, ellipsoid or subglobose, smooth, the endocarp woody, usually with resinous cavities, 5 foramina around apex and 5 oblong germinal valves on upper half; seeds oblong, usually 1–2 per fruit.

A genus of 12 species mostly in tropical South America with a single species reaching Costa Rica and Panama.

[3] Due to the poor herbarium representation of this family in Panama most descriptions are based in part on Cuatrecasas' excellent monograph.

FIGURE 1. *Humiriastrum diguense* (Cuatr.) Cuatr.—A. Inflorescence (× ¾).—B. Habit (× ½).—C. Flower (× 6).—D. Endocarp (× 1).—E. Fruit cross section (× 1). [After *Gentry 1938* (MO).]

1. **Humiriastrum diguense** (Cuatr.) Cuatr., Contr. U. S. Natl. Herb. 35: 141. 1961.—FIG. 1.

Sacoglottis diguensis Cuatr., Trop. Woods 96: 38. 1950. TYPE: Colombia, El Valle, *Cuatrecasas 14956* (F, holotype; VALLE, COL, G, US, isotypes).

Large *tree*, 25–30 m tall, the branchlets irregularly subangulate, puberulous. *Leaves* rigid-chartaceous, crenate, elliptic, acuminate, the base cuneate, 3.5–9.5 cm long and 2.2–5.2 cm wide, glabrous above, below with a few scattered inconspicuous trichomes; petiole 1–2 mm long, thickened at base. *Inflorescence* subterminal or terminal, cymose-paniculate, trichotomously branched, with the branches puberulous. *Flowers* with the sepals glabrous (in Panama) except for the ciliate margins, orbicular, ca. 1 mm long; petals oblong, obtuse, sparsely appressed puberulous outside; stamens 20, glabrous, the filaments connate at base, unequal, longer ones ca. 1.2 mm long, alternating with shorter series ca. 0.8 mm long, the anthers 0.7–0.8 mm long, connective very thick, ovoid-lanceolate, ob-

tuse, the 2 thecae elliptic, basal; disc formed by 0.2 mm scales; ovary conical, 1 mm long, pubescent, the style short, the stigma 5-lobate. *Drupes* (previously undescribed) elliptic-obovoid, obtuse at base and apex, 2.1–2.6 cm long and 1.1–1.5 cm in diameter, the exocarp coriaceous when dry, about 1 mm thick, the endocarp 2.0–2.5 cm long and 1.2–1.4 cm in diameter, woody, with small resiniferous cavities, surface fibrous, 5 deep holes at apex, these 3–5 mm long and alternating with 5 oblong descending opercula 6–8 mm long; usually 2 seeds developed.

Western Colombia to Costa Rica and Panama.

Cuatrecasas separated this species into two subspecies, subsp. *diguense* from the Pacific coast of Colombia and subsp. *costaricense* from the Golfo Dulce area of Costa Rica. He was able to examine only immature buds of subsp. *costaricense* which he distinguished on the basis of narrower leaves, subglabrous petals and more densely hirtellous branchlets and noted might prove a distinct species. The Panamanian specimens, intermediate geographically, are also morphologically intermediate having the hirtellous branchlets of subsp. *costaricense* and the noticeably but sparsely appressed puberulous petals of subsp. *diguense*. The leaves of one Panamanian collection (*Gentry 1938*) vary from 2.2–5.2 cm in width and are thus intermediate between those of *H. diguense* subsp. *diguense* var. *diguense* and *H. diguense* subsp. *costaricense*. (The few remaining leaves of the second collection seem somewhat smaller but are dead and wrinkled.) Since the distinctions between the two subspecies break down in geographically intermediate populations, I have not adopted Cuatrecasas' subspecies which are perhaps no more than varieties at best.

CANAL ZONE: Pipeline Road, premontane wet forest area, ca. 150 m, tree 18 inches diameter, 90 ft tall, petals green, anthers yellow, *Gentry 1938* (MO, SCZ). PANAMÁ: El Llano-Cartí-Tupile road, 12 mi. above Pan-Am Highway, primary forest, 200–500 m, large tree, collected from tree fall, *Liesner 1224* (F, MO, PMA).

2. SACOGLOTTIS

Sacoglottis Mart., Nov. Gen. Sp. Pl. 2: 146. 1827. TYPE: S. *amazonica* Mart.

Saccoglottis Endl., Gen. Pl. 1040. 1840.
Aubrya Baill., Adansonia 2: 265. 1862. TYPE: S. *gabonensis* (Baill.) Urb.

Trees. Leaves coriaceous or subcoriaceous, crenate or entire. *Inflorescence* axillary or subterminal, paniculate with dichotomous or trichotomous branching, the bracts persistent or deciduous. *Flowers* with sepals suborbicular, imbricate, more or less united at base; petals free, thick-membranaceous; stamens 10, glabrous, the 5 opposite sepals longer than alternate ones, the filaments thick, flattened, the thecae 2, unilocular, basal, the connective ovate-acuminate, acute; disc cupular, dentate; carpels opposite sepals, the ovary 5-locular, the cells uniovulate, the style as long as or exceeding stamens, the stigma capitate and 5-lobate. *Fruit* a medium-sized to large drupe, ellipsoid or subglobose, smooth, the endocarp woody, filled with resinous cavities, without foramina, the valves covering whole surface of endocarp so not apparent, with 10 very narrow, hardly visible longitudinal furrows; seeds oblong, usually 1–2 per fruit.

A genus of 10 species mostly in tropical South America; a single species is found in tropical West Africa and 2 species reach Costa Rica (including Cocos Island).

a. Drupe oblong-ellipsoid to oblong-ovoid, 3–4 cm by 2–2.8 cm, dry exocarp 1.0–3 mm thick, endocarp 5-ribbed; leaves with secondary veins thin, strongly ascending, slightly raised beneath; inflorescence pedunculate; ovary pubescent ... 1. *S. trichogyna*
aa. Drupe ovoid, 5–5.5 by 4–4.5 cm, dry exocarp 6–7 mm thick, endocarp without raised ribs; leaves with secondary veins relatively thick, not strongly ascending, prominently raised beneath; inflorescence subsessile; ovary glabrous ... 2. *S. ovicarpa*

1. **Sacoglottis trichogyna** Cuatr., Ciencia (Mexico) 27: 171. 1972. TYPE: Costa Rica, Heredia, *Holdridge 5216* (US).

Tree, the branchlets subterete, glabrous. *Leaves* rigid-chartaceous or thin-coriaceous, flexible, glabrous, elliptic, acuminate, obtusely cuneate at base, slightly crenate, 6.5–11.5 cm long and 2.5–5 cm wide, secondary nerves thin, slightly prominulous below, glabrous, drying grayish green; the petiole 8–11 (4–7, fide Cuatrecasas) mm long, grooved above, thickened at base. *Inflorescence* (after Cuatrecasas) paniculate, axillary, much shorter than the leaves, peduncle well-developed, the branchlets minutely hirtellous, the bracts ovate-triangular, ca. 1 mm long, deciduous. *Flowers* with the sepals orbicular, 1 mm long, eglandular, glabrous except the minutely ciliate margin; petals linear-oblong, glabrous, 5–6 mm long and ca. 1.5 mm wide, whitish green; stamens 10, glabrous, the filaments flattened, united at base, alternately 3 and 4 mm long, the anthers ovate-oblong, ca. 1 mm long, the thecae ca. 0.5 mm long, connective thick, subacute; disc surrounding ovary, denticulate, ca. 0.8 mm high; carpels 5, the ovary ovoid, ca. 1.5 mm high, villose-hispidulous, the style ca. 4 mm long, the stigma capitate, 5-lobate. *Drupe* oblong-ellipsoid to oblong-ovoid, 3–4 cm long, 2–2.8 cm in diameter, the exocarp smooth, 1–2 mm thick, the endocarp woody, with 5 raised ribs, filled with resinous cavities 1–4 mm in diameter, its surface pitted and rather warty; seed oblong, 1–3 per fruit.

Costa Rica and Panama.

Cuatrecasas first recorded this plant from Costa Rica as *S. amazonica* Mart. on the basis of sterile material. It differs from *S. amazonica* in puberulous inflorescence branchlets, eglandular sepals, and smaller fruits with 5-ribbed endocarps. The Panamanian collections are discussed and illustrated by Dwyer (Ann. Missouri Bot. Gard. 59: 252–254. 1972) under *S. ovicarpa*.

COLÓN: Salud, 120 m, dap. 19 cm y 18 m de alto, "conocillo," *Lao & Holdridge 193* (MO, PMA); 50 m, dap. 60 cm y 25 m de alto, "corotú," *Lao & Holdridge 195* (MO, PMA). Santa Rita Ridge 2 mi. from Trans-isthmian Hwy, tree with red inner bark and rounded, rather dense crown, *Lao, Holdridge & Gentry 5* (F, MO, PMA, SCZ).

2. **Sacoglottis ovicarpa** Cuatr., Trop. Woods 96: 39. 1950. TYPE: Colombia, Valle, *Cuatrecasas 19998* (F, holotype; VALLE, isotype).—FIG. 2.

Tree, the branchlets subterete, slightly puberulous or glabrate. *Leaves* rigid chartaceous to subcoriaceous, elliptic, more or less abruptly acuminate, rounded at base, drying reddish brown below, darker above, glabrous, very slightly cren-

FIGURE 2. *Sacoglottis ovicarpa* Cuatr.—A. Habit (× ½). [After *Liesner 1306* (MO).] —B. Fruit (× ½). [After *Holdridge 6271* (MO).]—C. Fruit cross section (× ½). [After *Cuatrecasas*.]

ulate, 9–20 cm long and 3.5–11.7 cm wide, midrib conspicuous above and below, the 9–11 pairs of secondary nerves conspicuous only below; the petiole thickened, 4–9 mm long. *Inflorescence* (previously undescribed) axillary, much shorter than the leaves, cymose-paniculate, dichotomous, very short, the peduncle obsolete, the branchlets reddish, slightly puberulous, bracts ovate-triangular, acute, tardily deciduous. *Flowers* (previously undescribed) with sepals suborbicular,

spreading, ca. 1.5 mm long, glabrous, the margin minutely and irregularly ciliate; petals oblong, about 3 mm long and ca. 1 mm broad, glabrous; stamens 10, united in lower half, glabrous, filaments compressed, alternately 1.5 and 2 mm long, the anthers ovoid, ca. 0.6–0.7 mm long, the thecae elliptic, ca. 0.3 mm long, connective thick, rather obtuse; disc not examined; carpels 5, the ovary ovoid, glabrous, style ca. 1 mm long, glabrous, the stigma capitate. *Drupe* (in part after Cuatrecasas) ovoid or ovoid-ellipsoid, 5–5.5 cm long and 4–4.5 cm wide, the exocarp 6–7 mm thick when dry, the endocarp woody, almost smooth, irregularly 5-septate, with abundant resinous cavities; seeds usually 1–2 per fruit.

Previously reported for Panama only from endocarps found in drift deposits on the shores of San José Island (Johnston, Sargentia 8: 52, 161; *pl. 10, fig. 3.* 1949), this species is known primarily from the Pacific coast of Colombia. A related species, *S. holdridgei* Cuatr. which was formerly included in *S. ovicarpa*, occurs on Cocos Island off Costa Rica.

The Panamanian collections agree fairly well with *S. ovicarpa* as described by Cuatrecasas, although the petioles are slightly shorter (8–14 mm in *S. ovicarpa*) and a few trichomes are present on parts of the branchlets of one collection (glabrous in *S. ovicarpa*). The flowers of *S. ovicarpa* have not previously been described. The flowering collection (*Liesner 1306*) has only a single small inflorescence with two mature flowers and a few buds so a complete dissection seemed inadvisable. *Inflorescence* and flowers are closer to those of *S. ceratocarpa* Ducke of the upper Amazon, especially in the subsessile inflorescence, than to *S. amazonica* with which Cuatrecasas keyed the species out. In addition to the key characters, this species differs from *S. trichogyna* in its larger darker-drying leaves.

COLÓN: Camp Betija, Donoso District, 60–150 m, tree 20 m tall, 25 cm dbh., *Holdridge 6271* (MO). SAN BLAS: Primary forest along newly cut road from El Llano to Carti-Tupile, continental divide to 1 mile from divide, 300–500 m, fallen branch in tree fall, *Liesner 1306* (MO).

3. VANTANEA

Vantanea Aubl., Pl. Guian. 1: 572, *pl.* 229. 1775. TYPE: *V. guianensis* Aubl.

Lemniscia Schreb., Gen. Pl., ed. 8. 1: 358. 1789.
Helleria Nees & Mart., Nov. Act. Acad. Nat. Cur. 12: 38, *pl.* 7. 1824.

Trees. Leaves coriaceous or subcoriaceous, entire or crenate. *Inflorescence* axillary or terminal, paniculate, usually dichotomous, also with alternate branching, the bracts deciduous. *Flowers* with sepals more or less united into a cupular calyx; petals free, thick, oblong or linear; stamens 50–180, in 3 or 4 rows, the filaments thin, glabrous, connate below in a tube surrounding the ovary, the anthers ovate-lanceolate, the thecae 2, bilocular, ellipsoid, attached at the lower side, the connective thick, ovate-oblong, acuminate to subobtuse; disc cupular, dentate or fimbriate; carpels opposite sepals, the ovary 5-locular, the cells biovulate, the style equalling or exceeding the stamens, the stigma more or less thickened, 5-lobate. *Fruit* a medium-sized or large drupe, ovoid or ellipsoid,

smooth, the endocarp woody, without resiniferous cavities, with 5 linear-oblong valves extending most of length of fruit; seeds oblong, usually 1–2 per fruit.

A genus of 14 species of mainland tropical America from Costa Rica to Santa Catarina, Brazil.

a. Petals pubescent, ca. 7 mm long; endocarp obtuse at both ends ..... 1. *V. barbourii*
aa. Petals glabrous, ca. 9 mm long; endocarp ellipsoid-attenuate at both ends, apically acute ..... 2. *V. occidentalis*

1. **Vantanea barbourii** Standl., Trop. Woods 75: 5. 1943. TYPE: Costa Rica, San José, *Dayton & Barbour 3129* (US, holotype; F, MO, isotypes).—FIG. 3A.

Tree, the branchlets angular, glabrous. *Leaves* coriaceous, entire, oblong-elliptic or elliptic, obtuse to emarginate, the base cuneate, 5–12 cm long and 2.4–6 cm wide, glabrous; petiole 6–10 mm long, flat above, thickened at base. *Inflorescence* axillary or subterminal, paniculate-cymose, as long as the leaves, the branches puberulous. *Flowers* with calyx 1–1.5 mm long, slightly puberulous, lobate, the lobes ciliate; petals white, oblong, subacute, adpressed retrorse-pubescent outside, ca. 7 mm long and ca. 2.5 mm wide; stamens 50–60, glabrous, the filaments 5–7 mm long, flattened, united at base, the anthers ovate-lanceolate, ca. 0.8 mm long with small lobes, the connective thick, acuminate-lanceolate; disc thick, 1 mm high, the margin short-denticulate; ovary ovoid, 1.5–2 mm high, densely tomentose-hirsute, the style 4 mm long. *Drupe* ovoid-oblong, smooth, obtuse at base and attenuate at apex, 2.8–3 cm long and 1.8–2 cm broad, the endocarp woody, ellipsoid-ovoid, ca. 2.7 cm long and 1.6 cm broad, obtuse at both ends, the valves 5, oblong, obtuse at apex, 1.8 cm long and 4–5 mm wide.

Known only from southern Costa Rica, but to be expected in adjacent Chiriquí Province, Panama.

2. **Vantanea occidentalis** Cuatr., Trop. Woods 96: 40. 1950. TYPE: Colombia, Valle, *Cuatrecasas 19937* (F, holotype; G, US, VALLE, isotypes).—FIG. 3B–C.

Large *tree* to 40 m, the branchlets glabrous. *Leaves* coriaceous, entire, oblong elliptic to obovate-elliptic, obtuse or subacuminate at apex, broadly cuneate at base, 7–16 cm long and 2.5–8.5 cm broad, glabrous; petiole 1–10 mm long, flattened above, thickened at base. *Inflorescence* (after Cuatrecasas) terminal, paniculate, shorter than the upper leaves, the branchlets dichotomously articulate, puberulous, bracts caducous. *Flowers* (after Cuatrecasas) with the sepals orbicular, subglabrous, 6–7 mm long, with a single gland outside; petals subcoriaceous, oblong, rather obtuse, glabrous, outside greenish white, inside white; stamens numerous (ca. 80), glabrous, the filaments unequal, ca. 8 mm long, linear, acute at apex, united at base, the anthers small, ovate-lanceolate, the connective thick at base, acute at apex; disc cupular, 1 mm high, minutely dentate; ovary 3–4 mm high, hirsute, the style 5 mm long. *Drupe* ovoid-ellipsoid, narrowed at both ends, ca. 3.5 cm long and ca. 1.8 cm thick, the endocarp woody, 2.2–3.3 cm long and 1.2–1.7 cm thick, ellipsoid-ovoid, acute at apex, tapering to a rounded base, surface rather smooth with 5 broad ribs alternating with 5 oblong valves, 1.8–2.1 cm long and 3–4 mm wide; seed oblong, 1 per fruit.

FIGURE 3. *Vantanea*.—A. *V. barbourii* Standl., habit ($\times$ 7/10). [After *Dayton & Barbour 3129*, Costa Rica (MO).]—B–C. *V. occidentalis* Cuatr.—B. Endocarp ($\times$ 1^2/$_5$).—C. Endocarp cross section ($\times$ 1^2/$_5$). [After *Gentry 1931*.]

Western Colombia to Panama.

This species is one of the most important large trees in premontane wet forest and tropical wet forest of central Panama. The fragmentary collections of such an important species of the "well-collected" Canal Zone is indicative of the paucity of our present knowledge of wet forest Panamanian trees.

The endocarp of the Panamanian collections is acute at the apex and matches that of *V. occidentalis* of Colombia rather than the obtuse endocarp of Costa Rican *V. barbourii*. However, a few of the endocarps are rather blunt-ended and approach *V. barbourii*. The dimensions of the Panamanian endocarps (2.2–3.3 cm long) more than span the size ranges given for both *V. barbourii* (2.7 cm) and *V. occidentalis* (3–3.3 cm). In the absence of flowering material from Panama Cuatrecasas' key character of pubescent petals in *V. barbourii* versus glabrous petals in *V. occidentalis* cannot be checked.

CANAL ZONE: Pipeline road premontane wet forest area, fruits and leaves from ground beneath giant tree 2½ feet diameter and 100 feet tall, *Gentry 1931* (MO); fallen leaves and fruits from 35 m tree, *Gentry 7406* (MO).

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FLORA OF PANAMA[1]

BY ROBERT E. WOODSON, JR. AND ROBERT W. SCHERY
AND COLLABORATORS

Part VI

FAMILY 103. CELASTRACEAE[2]

GABRIEL EDWIN[3] AND DING HOU[4]

Trees, *shrubs*, or *lianas*. *Leaves* alternate or opposite, simple; stipules small and caducous. *Inflorescences dichasial*, less often paniculate, racemose, or borne singly. *Flowers* bisexual or unisexual; calyx 4- or 5-lobed, mostly imbricate, persistent; petals 4 or 5, usually, imbricate, attached under the margin of the disc; stamens 4 or 5, alternate with the petals, inserted at or under the margin of the disc, anthers 2-celled; disc cup-shaped, or flat and fleshy, lobed or entire; ovary free from or adnate to the disc, 2- to 5-loculed (locules sometimes aborting), each 2- or 1-ovuled, occasionally to 8-ovuled, ovules erect or pendulous, style short or lacking, stigmas lobed or blunt. *Fruit* a capsule, drupe or samara; seeds usually arillate.

The family includes 53 genera and about 500 species widely distributed in the tropics, but less common in temperate regions.

Literature:

Brizicky, G. K. The genera of Celastrales in the southeastern United States. Jour. Arnold Arboretum 45: 206–234. 1964.

Loesener, T. Celestraceae. *In* A. Engler & K. Prantl., "Die natürlichen Pflanzenfamilien." Ed. 2. 20b: 87–197. 1942.

Lundell, C. L. Celastraceae. *In* "Studies of American plants." Wrightia 4: 178. 1971.

a. Plant scandent; ovary free from the disc ..... 1. *Celastrus*
aa. Plant erect; ovary joined to the disc.
  b. At least some of the flowers bisexual; the ovules erect; leaf apex not emarginate.
    c. Inflorescences distinctly dichasial, solitary, or fasciculate; fruit an indehiscent drupe or samara; seeds exarillate.
      d. Flowers, at least some of them, 4-merous; fruit a drupe ..... 2. *Crossopetalum*
      dd. Flowers 5-merous; fruit a samara.
        e. Leaves opposite ..... 3. *Zinowiewia*
        ee. Leaves alternate ..... 4. *Wimmeria*

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[1] Assisted by National Science Foundation Grant GB-36202X (Thomas B. Croat, principal investigator).

[2] This treatment is based on a draft prepared in 1956 by Ding Hou. It was recently revised for publication by Gabriel Edwin.

[3] Roosevelt University, Chicago, Illinois 60605.

[4] Rijksherbarium, Leiden, Netherlands.

cc. Inflorescences fasciculate; fruit a dehiscent capsule; seeds arillate ..... 5. *Maytenus*

bb. Flowers all unisexual; the ovules pendulous; leaf apex slightly emarginate ..... 6. *Gyminda*

1. CELASTRUS

Celastrus L., Sp. Pl. 196. 1753; Gen. Pl., ed. 5. 91. 1754. TYPE: *C. scandens* L.

Scandent *shrubs*. *Leaves* deciduous, alternate, petiolate. *Inflorescences* dichasial, paniculate to racemose, solitary, axillary and/or terminal, pedunculate or sessile; pedicels articulated. *Flowers* usually unisexual and plants dioecious (bisexual in the Latin American species); calyx 5-lobed; petals 5; disc cup-shaped or fleshy and flat, entire or 5-lobed, stamens 5; ovary superior, free from the disc, 3-loculed, each 1-ovuled (in the Latin American species), ovules attached at the base of the ovary with a distinct cup-shaped aril towards the base. *Fruit* a capsule, 1- to 6-seeded; seeds enclosed in a fleshy crimson aril.

About 31 species distributed chiefly in tropical and subtropical Asia and America.

1. **Celastrus panamensis** Lundell, Contr. Univ. Michigan Herb. 6: 40. 1941. TYPE: Panama, *Allen 319* (MO).—FIG. 1.

Leaves ovate, apically obtuse, basally rotund, the margins shallowly crenate, 9–14 cm long and 5.0–7.5 cm wide, membranous, the primary lateral veins in 7 or 8 pairs, elevated beneath, plane and distinct above; petiole 11–13 mm long. *Inflorescences* axillary as well as terminal, to 7 cm long, usually twice-forked; the primary peduncle glabrous, 1.2–2.5 cm long; the pedicels ca. 1 mm long. *Flowers* bisexual, white; calyx lobes orbicular, obtuse, minutely erose, ca. 1.2 mm in diameter; petals oblong, rotund, more or less entire, ca. 2 mm long and 1.2 mm wide; disc fleshy, flat, slightly 5-lobed; stamens ca. 2 mm long; pistil short, conoid, ca. 1.5 mm long, the style columnar and blunt. *Fruit* not seen.

Known only from Panama, this species flowers in April.

PANAMÁ: Chiriquí, *Allen 319* (MO).

2. CROSSOPETALUM

Crossopetalum P. Browne, Civ. Nat. Hist. Jamaica 145, *t. 17. f. 1.* 1756. TYPE: *Rhacoma crossopetalum* L. = *Crossopetalum rhacoma* Crantz.

Rhacoma L., Syst. Nat., ed. 10. 2: 896. 1759. TYPE: *R. crossopetalum* L.

Shrubs or small *trees*. *Leaves* opposite, alternate, or rarely ternate. *Inflorescences* dichasia, axillary. *Flowers* bisexual; calyx 4-lobed; petals 4; disc cup-shaped, slightly 4-lobed; stamens 4, inserted between the lobes of the disc; pistil semi-inferior by adhesion to the disc, ovary 4-loculed (or 2-loculed?), each 1-ovuled. *Fruit* a drupe; seed exarillate.

This genus includes about 36 species distributed in tropical America and West Indies.

FIGURE 1. *Celastrus panamensis* Lundell.—A. Flowering branch (× ½).—B. Flower bud (× 10).—C. Gynoecium (× 10).—D. Disc and anthers, perianth removed (× 10). [After *Allen 319* (MO).]

1. **Crossopetalum eucymosa** (Loes. & Pitt.) Lundell, Wrightia 3: 7. 1961.—FIG. 2.

Myginda eucymosa Loes. & Pitt., Contr. U. S. Natl. Herb. 12: 175, *pl. 18*. 1909. TYPE: Guatemala, *Pittier 239* (US).
Rhacoma eucymosa (Loes. & Pitt.) Standl., Carnegie Inst. Washington Publ. 461: 6. 1935.

FIGURE 2. *Crossopetalum eucymosa* (Loes. & Pitt.) Lundell.—A. Flowering branch (× 1⅔).—B. Flower, part of perianth removed (× 10). [After *Johnston 1718* (MO).]

Small *trees* to 5 m tall. Leaves ovate-elliptic, apically acuminate, basally broadly cuneate, the margins obscurely revolute, serrulate to entire, 5–10 cm long and 2–4 cm wide, the primary lateral veins in 4–6 pairs, pallid and slightly elevated beneath, evident and dark green above; petiole 5 mm long. *Inflorescences* 2 cm long, 3- or 4-times-forked; peduncles puberulent, the primary peduncle 1.0–1.5 cm long; pedicels 2 mm long, puberulent. *Flowers* with the calyx 4-lobed, the lobes orbicular, 1 mm in diameter, puberulent outside; petals obovate, 2.5 mm long and 1 mm wide, rounded apically, attenuate into a short claw; disc cup-shaped, 4-lobed; stamens 4, attached between the lobes of the disc, filaments slender, 1.5 mm long, anthers subreniform, extrorse, sometimes twisting to an introrse orientation; ovary 2-loculed, 1-ovuled, the style short, the stigma 2-lobed. Fruit a subglobose drupe, ca. 12 mm in diameter.

This species ranges from sea level to 120 m in Central America. It flowers from April to August.

Loesener (1942) separated *Crossopetalum* (as *Rhacoma*) from *Myginda*, but Brizicky (1964) treated the two as synonymous. According to Loesener's key to genera, *Crossopetalum* has a 4-loculed ovary and the seed contains endosperm, while *Myginda* has a 2-loculed ovary and no endosperm. Loesener did not mention the species treated here. The specimens cited are in flower, the ovary is 2-loculed, and each locule is 1-ovuled. Thus following Loesener, the species should be included in *Myginda*.

CANAL ZONE: Devil's Beach, *Johnston 1718* (MO). PANAMÁ: Province of Bocas del Toro, Isla Colón, *Wedel 571* (GH, MO). COLÓN: Río Indio de Fató, *Pittier 4255* (F, GH, US).

3. ZINOWIEWIA

Zinowiewia Turcz., Bull. Mosc. 1: 275. 1859. TYPE: *Z. integerrima* (Turcz.) Turcz.

Shrubs or small *trees*. *Leaves* opposite, petiolate. *Inflorescences* axillary, fasciculate. *Flowers* bisexual; calyx 5-lobed, lobes rotund; petals 5; stamens 5; disc fleshy, annular, slightly 5-lobed; ovary semi-inferior, adnate to the disc, 2-loculed, each 2-ovuled, the style short, conic, the stigma obscure, 2-lobed. *Fruit* a samara.

This genus includes about 7 species distributed from southern Mexico to Venezuela.

1. **Zinowiewia costaricensis** Lundell, Bull. Torrey Bot. Club 65: 471. 1938. TYPE: Costa Rica, *Tonduz 7861* (US).—FIG. 3.

Zinowiewia ovata Lundell, Bull. Torrey Bot. Club 67: 620. 1940. TYPE: Panama, *Maxon 5109* (F).

Trees to 13 m tall. *Leaves* usually elliptic on the current season's branchlets, or ovate on the older branchlets, apically acuminate, basally cuneate, the margin entire, 3–6 cm long and 1.2–3.2 cm wide, the primary lateral veins 4–6 pairs, slightly elevated beneath, evident above; petiole 3–6 mm long. *Inflorescences* axillary, ca. 2 cm long, 3- to 4-times-forked; the primary peduncle 5–10 mm long; pedicels 2 mm long. *Flowers* with calyx 5-lobed, lobes orbicular, 0.5 mm in diameter; petals 5, broadly ovate, rounded apically, 1.5 mm long and 1 mm wide; disc nearly flat, unlobed; pistil conical, the style pointed. *Fruit* oblanceolate, subfalcate, 2 cm long and 0.8 cm wide, apically emarginate, the venation netted on the wing, usually 1-loculed and 1-seeded; seed linear-oblong, 6–8 mm long.

This species occurs in Costa Rica and Panama from 1000–1500 m. It flowers from March to April.

Lundell (1971) cited two collections not seen in this study: Chiriquí, *Proctor 31876, 31999* (both LL).

CHIRIQUÍ: Escuela San Benito, *Croat 10420* (MO). Bajo Mono Boquete, *Davidson 519* (F, MO). Near El Boquete, *Maxon 5109* (F). Cerro Horqueta, *Pittier 2858* (US); *Dwyer & Hayden 7715* (MO). Way to Lerida, *Maurice 901* (US). Llanos just S of town, *Stern et al. 1945, 1949* (both MO). Finca Collins, *Stern et al. 1092* (?). Llanos Francia, *Stern et al. 1219* (MO). COLÓN: 10 mi. SW of Portobelo, *Liesner 1052* (MO). PANAMÁ: Calzada Larga, *Lao & Holdridge 49* (MO).

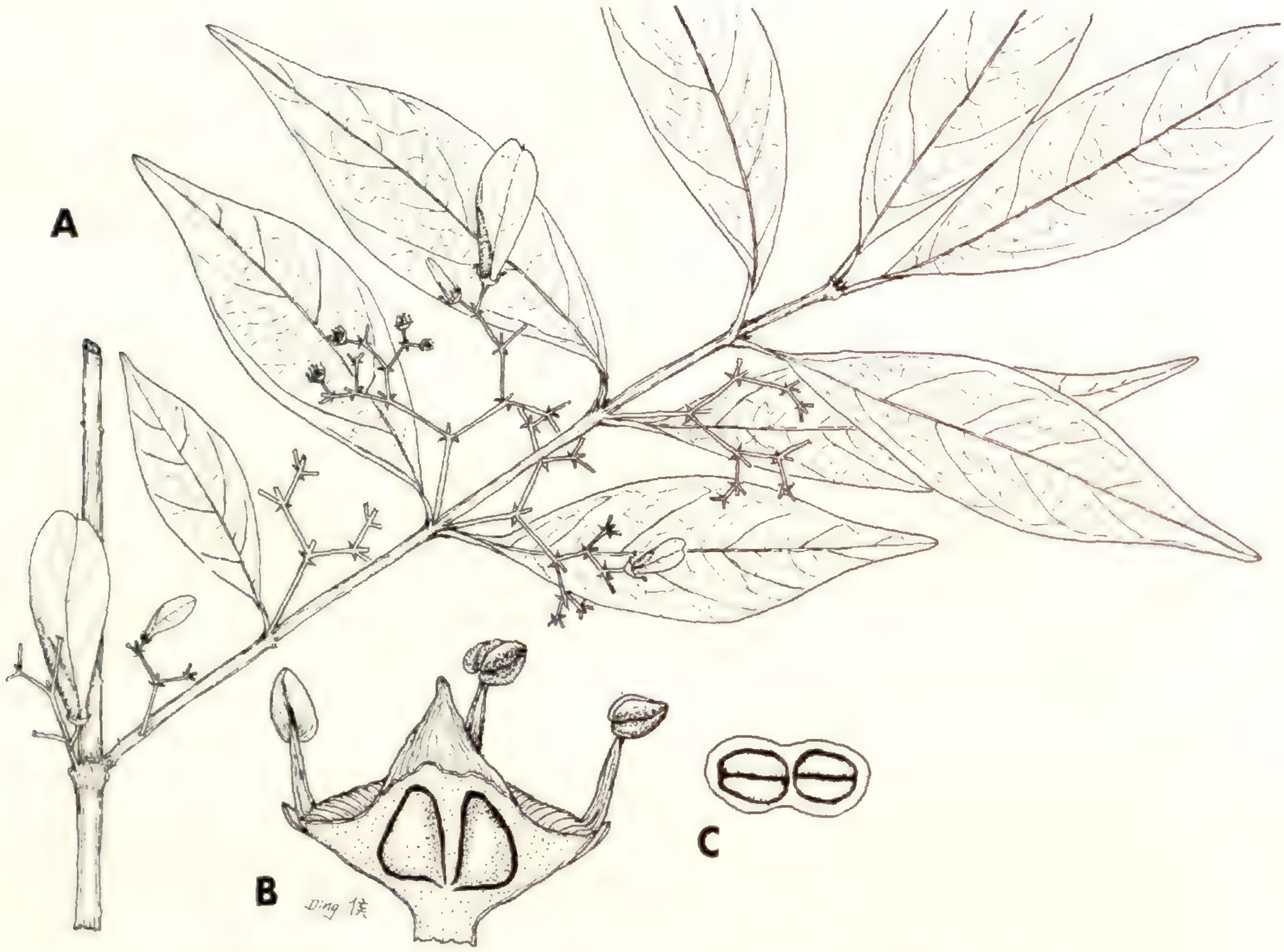

FIGURE 3. *Zinowiewia costaricensis* Lundell.—A. Flowering branch (× 1).—B. Cross section of flower showing gynoecium and androecium (× 20).—C. Cross section of ovary showing arrangement of ovules (× 20). [After *Davidson 519* (MO).]

4. WIMMERIA

Wimmeria Schlecht. & Cham., Linnaea 7: 427. 1831. TYPE: *W. concolor* Schlecht. & Cham.

Essentially glabrous *tree*. *Leaves* alternate or subopposite at the apices of branchlets, petiolate; pedicels short. *Flowers* perfect, regular, 5-merous; perianth imbricate; calyx subobsolete, the lobes obtuse; petals inserted below the disc, sessile, shorter than or as long as the stamens; anthers dorsifixed, laterally dehiscent; disc fleshy, lobed; ovary adnate to the disc at the base, pyramidate-trigonous, 3-locular, 2 (or more) ovules per locule, basifixed, the style short, the stigma 3-lobed. *Fruit* a triquetrous samara, the endocarp papery, 1-seeded, 1-loculate by abortion.

This genus ranges from Brazil north to Panama and Guatemala.

1. **Wimmeria sternii** Lundell, Trop. Woods 110: 29, *fig. 1*. 1959. TYPE: Panama, *Stern & Chambers 57* (MO, isotype).—FIG. 4.

Glabrous *tree* with reddish slender branchlets. *Leaves* mostly lanceolate, 3.3–7.8 cm long and 1.0–2.5 cm wide, narrowed to base and apex, the margin serrulate, the costa apparent above and beneath; petiole 3–8 mm long, ridged

above. *Inflorescences* forming cymes; peduncles slender, (1–)3(–7)-flowered; pedicels jointed at base. *Flowers* and fruits not seen.

This species is known only from the type collection.

CHIRIQUÍ: Cloud forest, foothills of Volcán Baru, NW of El Hato, 4500 ft, *Stern & Chambers 57* (MO).

5. MAYTENUS

Maytenus Molina, Saggio Stor. Nat. Chile 177. 1782. TYPE: *M. boaria* Molina.

Shrubs or small *trees*. *Leaves* usually alternate, distichous, entire or serrate, coriaceous, petiolate; stipules small. *Inflorescences* fasciculate, bracteolate, axillary or caulinary. *Flowers* bisexual, 5-merous; calyx lobes and petals imbricate; disc fleshy, thick, annular; stamens attached on the margin of the disc; pistil semi-inferior by adnation, 2- or 4-loculed, each 1- or 2-ovuled, rarely with obscure aril at the base. *Fruit* a capsule, 1- to 3-loculed, 1- to 3-seeded; the seed included in an incomplete aril.

This genus includes about 200 species distributed chiefly in tropical and subtropical America, some in South Pacific, Asia, Malaysia and Africa, and 4 species in Panama.

a. Leaves obovate, lanceolate-elliptic, or elliptic, at least 3 times longer than wide.
  b. Leaves obovate to elliptic, basally attenuate, to 3 times longer than wide, the margins crenate ..... 1. *M. woodsonii*
  bb. Leaves elliptic or lanceolate-elliptic, 3.5 times longer than wide ..... 2. *M. longipes*
aa. Leaves broadly elliptic, obovate, or ovate, mostly (?always) less than 3 times longer than wide.
  c. Margins regularly crenulate below, teeth scattered above ..... 3. *M. guyanensis*
  cc. Margins entire, sinuate, finely crenulate-serrulate, or with few scattered teeth ..... 4. *M. schippii*

1. **Maytenus woodsonii** Lundell, Ann. Missouri Bot. Gard. 26: 291, *tab.* 22. 1939. TYPE: Panama, *Woodson et al. 1065* (MO, isotype).—FIG. 5.

Maytenus vulcanicola Standl., Field Mus. Pub. Bot. 22: 153. 1940. TYPE: Panama, *Terry 1309* (F, holotype; MO, isotype).

Shrubs or small *trees*, to 5 m tall; branchlets verticillate. *Leaves* alternate, subverticillate at the apex of the branchlets, obovate, elliptic, apically rounded, rarely acute, basally broadly cuneate, the margins serrulate, 4–8 cm long and 1.5–4.0 cm wide, coriaceous, the primary lateral veins in 6–9 pairs, slightly elevated beneath, evident above. *Inflorescences* axillary or caulinary, fasciculate, bracteoles persistent at the base of the pedicel, maroon, laciniate; the pedicels about 5 mm long. *Flowers* with the calyx deeply 5-lobed, the lobes imbricate, semiorbicular, ciliate, 1.2–1.8 mm long; petals broadly ovate or suborbicular, ca. 2.5 mm long, ciliate; disc fleshy, thick, slightly discoid; stamens 5, anthers ovoid-oblong, ca. 0.7 mm long, filaments short; pistil semi-inferior by adnation, the style obscure. *Fruit* a capsule, orbicular or slightly obovoid, 7 mm in diameter; seeds 1–3, 6 mm long and 3 mm wide, incompletely arillate.

This species occurs in Panama from 2500–4000 m. It also occurs in Costa Rica. It flowers from February to July.

FIGURE 4. *Wimmeria sternii* Lundell, flowering branch (× 1⅛). [After *Stern & Chambers 51576* (MO).]

CHIRIQUÍ: Summit SW face of Cerro Copete, 9000 ft, *Allen 4885* (MO). Volcán de Chiriquí, Potrero Muleto, 10,400 ft, *Davidson 1053* (MO); 11,200 ft, *Terry 1309* (F, MO). Loma Larga to summit Volcán de Chiriquí, 2500–3380 m, *Woodson et al. 1065, 1088* (both MO). Potrero Muleto to summit of Volcán de Chiriquí, *Woodson & Schery 398, 440* (both MO).

2. **Maytenus longipes** Briq., Ann. Conserv. Jard. Bot. Genève. 20: 361. 1919. TYPE: Colombia, Santa Marta, *Smith 454* (G).

Trees or *shrubs* with glabrous crowded branchlets. *Leaves* glabrous, short petiolate, elliptic to lanceolate-elliptic, 6.0–9.0 cm long and 2.3–3.8 cm wide,

with an obtuse acumen, entire or subentire, basally acute; petiole glabrous, to 5 mm long; stipules minute, triangular, obscurely ciliolate. *Inflorescences* many-flowered, flowers solitary or fasciculate; pedicels to 5–6 mm long, much longer than the flowers. *Flowers* 5-parted; sepals 0.5 mm long, ovate; petals obovate, 1.5 mm long and 1.2 mm wide, obtuse, or minutely apiculate; disc 5-lobulate; filaments longer than the small, cordate anthers; ovary immersed in the disc.

PANAMÁ: Cerro Azul, *Dwyer 1897* (MO).

3. **Maytenus guyanensis** Klotsch & Schomb., Fauna Fl. British Guiana 1097. 1848 [1849].

3a. **Maytenus guyanensis** f. **crenulata** Steyerm., Fieldiana, Bot. 28 (2): 338. 1952. TYPE: Venezuela, Anzoátegui, *Steyermark 61731* (F).

Tree to 30 ft, essentially glabrous. *Leaves* broadly elliptic, subcoriaceous, thin to firmly membranaceous, the margins crenulate; petioles short, thickened; stipules subdeltoid. *Cymes* subsessile to short peduncled. *Flowers* with the calyx lobes subacute, laciniate. *Fruit* subcompressed, obovoid.

The typical variety has entire leaves. It is generally distributed in the West Indies and parts of South America.

CANAL ZONE: SE shore of Barro Colorado Island, *Hayden 144* (MO). DARIÉN: Near Campamento Buena Vista, Río Chucunaque above conflux with Río Tuquesa, *Stern et al. 863* (MO).

4. **Maytenus schippii** Lundell, Phytologia 1: 305. 1939. TYPE: Belize, *Schipp 1014* (MICH).

Glabrous *tree* to 10 m high, branchlets slender. *Leaves* thinly subcoriaceous, obovate to elliptic, 5.0–11.5 cm long and 2.3–5.4 cm wide, abruptly acuminate, the acumen obtuse, the base broadly cuneate, finely crenulate-serrulate, the costa elevated above and beneath; petioles canaliculate, 6–9 mm long. *Inflorescences* axillary, fasciculate; pedicels 4–6 mm long. *Flowers* with 5 dentate calyx lobes. *Capsules* bright orange, obovoid, 9–12 mm long, 2-celled with 2 erect ovules per cell, but 1–3-seeded at maturity; aril red.

This species is close to *M. guatemalensis* Lundell, according to Lundell's protologue, and probably also close to *M. jamaicensis* Kr. & Urb.

CANAL ZONE: Barro Colorado Island, *Croat 6135* (MO). Third small cave E of Slothia Island, *Croat 6123* (MO). Between Bat Cave and Colorado Point, *Foster 1196* (MO). COLÓN: Salud, *Lao & Holdridge 231* (MO).

6. GYMINDA

Gyminda Sarg., Gard. For. 4: 4. 1891. TYPE: *G. latifolia* (Sur.) Urb.

Dioecious *shrubs* or *trees*. *Leaves* opposite, coriaceous; stipules small, caducous. *Inflorescences* axillary, pedunculate dichasia. *Flowers* unisexual; sepals 4, small; petals 4; disc annular or quadrate, fleshy; male flowers with 4 stamens inserted on the margin of the disc, filaments subulate, anthers oblong, introrse; pistil rudimentary, conic, 2-lobed; female flowers with ovoid pistil, ovary ob-

A
B
C
D
E
F
Ding 侯

FIGURE 6. *Gyminda costaricensis* Standl.—A. Flowering branch (× 1⅕).—B. Flower (× 12).—C. Androecium and gynoecium, perianth removed (× 12).—D. Cross section of ovary showing arrangement of ovules (× 12).—E. Longitudinal section of ovary (× 12).—F. Longitudinal section of apical portion of young fruit (× 12).—G. Mature fruit (× 3). [After *Woodson et al. 900* (MO).]

long, basally adnate to the disc, 2-loculed, each locule 1-ovuled, the ovules pendulous, the style short, the stigma 2-lobed. *Fruit* a drupe, usually 1-seeded.

This genus comprises 4 species of West Indies and Central America.

1. **Gyminda costaricensis** Standl., Field Mus. Publ. Bot. 18: 632. 1937. TYPE: Costa Rica, *Standley & Valerio 49568* (F).—FIG. 6.

Trees up to 20 m tall. *Leaves* elliptic, apically obtuse, slightly emarginate, basally cuneate, the margins crenate-serrulate at the upper half, 3–9 cm long and 1.5–4.5 cm wide, the primary lateral veins 5–7 pairs, slightly elevated beneath, distinct above; petiole 1–4 mm long. *Inflorescences* axillary dichasia, usually

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FIGURE 5. *Maytenus woodsonii* Lundell.—A. Flowering branch (× ⅗).—B. Opening flower bud (× 6).—C. Cross section of flower showing gynoecium and androecium (× 12).—D. Fruiting capsule (× 1⅘).—E. Seed enfolded by aril (× 3).—F. Seed, aril removed (× 3). [A–C after *Woodson et al. 1065* (MO). D–F after *Terry 1309* (MO).]

4-forked; the primary peduncle 5–8 mm long; pedicels very short, 2-bracteolate. *Flowers* with the sepals deltoid to rotund in two opposite pairs, 0.5 mm long, minutely ciliate; petals white, ovate-oblong, 2 mm long and 0.5 mm wide; disc quadrate, fleshy; male flowers with stamens 1 mm long; female flowers with pistil 2 mm long, stigmas 2-lobed, flat. *Fruit* a drupe, oblong or slightly obovoid, 7 mm long, 3 mm in diameter.

This species occurs in Costa Rica and Panama from 1500–2000 m. It flowers in January.

CHIRIQUÍ: Near Casita Alta, Volcán de Chiriquí, *Woodson et al. 900* (GH, MO, NY). Near "New Switzerland," central valley of Río Chiriquí Viejo, *Allen 1401* (GH, MO, NY, US).

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FLORA OF PANAMA[1]

BY ROBERT E. WOODSON, JR. AND ROBERT W. SCHERY
AND COLLABORATORS

Part VI

FAMILY 107. HIPPOCASTANACEAE

W. G. D'ARCY[2]

Trees or *shrubs*, the twigs terete or elliptical and grooved. *Leaves* opposite and digitately compound (rarely alternate and pinnate in seedlings and turoins), deciduous or persistent, the buds mostly large, often resinous and with bud scales; leaflets 3–11, membranaceous or coriaceous, pinnately veined, the margins entire or variously toothed or sinuate, estipulate. *Inflorescence* a terminal racemose or cymose panicle, the upper flowers mostly staminate with a stipitate, reduced ovary, the perfect flowers below, bracts resembling foliage leaves or much reduced, bracteoles usually present at the base of the articulated pedicel and subtending the point of articulation. *Flowers* showy, white, red or rarely yellow, the axis oblique to the plane of the inflorescence; sepals 5, equal or unlike, fused for more than half their length or essentially free, quincuncial in bud, caducous; petals 4–5 alternating with the sepals, free, unequal, often with a claw; disc extrastaminal, annular or mostly irregular in shape; stamens 5–8 in 2 whorls, the outer opposite the sepals and partly aborted, the filaments elongate and arcuate, the anthers exserted, the two parallel locules introrse; the fertile ovary superior, often sessile, 3-carpellate, (2–)3(–4)-locular with 2 axile, amphitropous ovules in each locule, the upper ascending and apotropous, the lower descending and epitropous, an aril present at early stages, the styles united and the stigma entire or obscurely 3-lobed. *Fruit* a leathery, mostly 3-valvate, locucidally dehiscent capsule, sometimes spiny; seed large, globose or somewhat flattened, smooth, shiny, black, nut-like, the embryo large and the cotyledons unequal, endosperm wanting.

Hippocastanaceae *nom. cons.* include 2 genera, *Aesculus* with about 13 species of the North Temperate zone, and *Billia* with 2 species of tropical America. The Hippocastanaceae differs little from the Sapindaceae and may not warrant separate family status. The opposite, digitate leaves, the usually irregular disc, the incomplete outer whorl of stamens and the presence of perfect flowers are the principal features of the Hippocastanaceae which differ from the Sapindaceae. The two families appear to be linked by the genera *Ungnadia* of Mexico and *Bretschneidera* of China which display similarities to both families. Hardin, who revised the American species, believed that the group has a southern origin

[1] Assisted by National Science Foundation Grant GB-5674 (Thomas B. Croat, principal investigator).

[2] Missouri Botanical Garden, 2315 Tower Grove Avenue, St. Louis, Missouri 63110.

ANN. MISSOURI BOT. GARD. 62: 57–60. 1975.

and that in the Hippocastanaceae *Billia* is more primitive than the larger northern genus *Aesculus*.

The family is of slight economic importance, a number of species being cultivated as ornamentals. There are reports of the fruits (or seeds) of some species being poisonous to livestock. Most parts of the plants and honey made from the nectar of some species are reported to contain a poisonous glucoside.

Literature:

Hardin, J. W. A revision of the American Hippocastanaceae. Brittonia 9: 145–171; 173–195. 1957.

1. BILLIA

Billia Peyr., Bot. Zeit. 16: 153. 1858. TYPE: *B. hippocastanum* Peyr.

Putzeysia Planch. & Lind. *in* Lind., Cat. Hort. 22: 3. 1857, nomen nudum.

Trees to 30 m tall, the crown rounded or spreading. *Leaves* trifoliolate, deciduous or persistent; the leaflets coriaceous, glabrate, shiny above, pinnately veined, ovate or elliptic with an acuminate, ultimately blunt drip tip, the margins entire; petioles glabrate, shorter than the leaflets with an expanded, slightly clasping base, the petiolules short. *Inflorescence* a showy, many-flowered panicle to 25 cm tall with decussate branching terminating in dichasia, the bracts mostly resembling the foliage leaves, the small bracteoles leaving conspicuous rings around the axes. *Flowers* colorful; sepals often red or purple, essentially free, quincuncial in bud and imbricated at the base, mostly unequal, ovate to oblong; petals red or white with a yellow or pink base, 4(–5), 8–25 mm long, mostly with a basally pubescent claw, the upper pair longer than the lateral pair; disc mostly eccentric and trilobed; stamens 6–8, filaments often colored, 20–30 mm long, arcuate-ascending, the anthers yellow, long exserted, glandular at the ends of the locules; ovary deep pink, glabrous or pubescent, stipitate, oblong fusiform. *Fruit* a leathery smooth or slightly scaly moderately angled capsule, 5–8 cm long; seeds 1–3, 3–5 cm in diameter, dark brown or black.

A tropical American genus of 2 species occurring mostly in upland areas. The species overlap ranges in Costa Rica, *B. hippocastanum* extending north to Oaxaca and Vera Cruz and *B. columbianum* extending south and east to Ecuador and Venezuela. The trees are attractive in shape and showy in flower.

Sterile collections of members of this genus may be confused with specimens of *Caryocar microcarpum* Ducke (Caryocaraceae), a species which grows in eastern South America. Specimens of *Caryocar* may often be distinguished by the large, narrowly conical, peg-like vegetative tips and by the frequent presence of large (to 3 mm) extra-floral nectaries in the axils of the leaflets. The flowers and fruits in the two genera are quite different.

1. **Billia columbianum** Planch. & Lind. *in* Triana & Planch., Ann. Sci. Nat. Bot., sér. 4. 18: 366. 1862. TYPE: Colombia, *Triana* 1866 (G, not seen; MO, photo; ?MPU).—FIG. 1.

FIGURE 1. *Billia columbianum* Planch. & Lind.—A. Flowering branch (× ½). [After *D'Arcy & D'Arcy 6444* (MO).]—B. Fruit (× ⅛). [After *Lawrance 394* (MO), Colombia.]

Putzeysia rosea Planch. & Lind. *in* Lind., Cat. Hort. 22: 3. 1857, nomen nudum.

Tree to 10 m tall, the twigs elliptical in cross section. *Leaves* digitately 3-foliolate, coriaceous, mostly glabrous; the leaflets to 12 cm long, ovate or elliptical, apically acuminate and ultimately blunt in a drip tip, basally obtuse, acute or acuminate, the margin entire, veins 6–11 on each side of the midvein, inconspicuous or light colored above, usually prominent and often purplish beneath; petiole half as long as the leaflets or shorter, slightly clasping the twigs, conspicuously winged on emerging but the wings not evident at maturity, petiolules short. *Inflorescence* pyramidal or corymbiform, to 30 cm long, subtended by a series of leaf-like bracts, the axis, branches and pedicels densely puberulent, one of each pair of flowers usually abortive; the pedicels 10–15 mm long, articulating near the base, the articulation point subtended by a bracteole and an abortive bud. *Flowers* very fragrant, showy; the sepals mostly purple, sometimes with patches of yellowish or grey tomentum, oblong to orbicular, imbricated at the

base and minutely ciliate, nearly alike or quite unlike, the inner pair mostly longer and broader; petals showy white with a yellow and pink or orange eye at the base, drying with conspicuous veins, often partly pubescent, 8–20 mm long, spatulate, somewhat unequal; stamens 6–8, the filaments 20–30 mm long, often unequal, colored or not; the fertile ovary glabrous with a pubescent style. *Fruit* a leathery, thick-walled, tardily dehiscent capsule; seed large with starchy cotyledons.

This species ranges from Costa Rica to Venezuela and Ecuador, occurring usually as isolated trees at middle and upper elevations. *Billia hippocastanum* Peyr., which occurs in neighboring, Costa Rica differs from *B. columbianum* in its deep red flowers and glabrous inflorescences. The species are difficult to separate without flowers and the *Hagen & Hagen* collection cited below may actually be *B. hippocastanum*.

CHIRIQUÍ: Tree in pasture above Boquete at La Popa, 5800 ft, *D'Arcy & D'Arcy 6444* (MO). Rain forest, Bajo Chorro, Boquete District, 6000 ft, *Davidson 234* (MO). Dense woodland & cloud forest, *Dwyer & Hayden 7687* (MO). Cloud forest, Cerro Horqueta, 6500 ft, *Hagen & Hagen 2139* (MO). Near Bajo Chorro, 1900 m, *Woodson & Schery 672* (MO).

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FLORA OF PANAMA[1]

BY ROBERT E. WOODSON, JR. AND ROBERT W. SCHERY
AND COLLABORATORS

Part VIII

FAMILY 160. GENTIANACEAE[2]

THOMAS S. ELIAS[3] AND ANDRÉ ROBYNS[4]

Annual or perennial *herbs*, rarely subshrubs or shrubs, sometimes saprophytic and then without chlorophyll, usually erect, rarely climbing or epiphytic, the branches usually dichotomous, glabrous throughout. *Leaves* opposite, decussate, often connate at the base, simple, entire, estipulate, usually cauline, sometimes in basal rosettes, rarely reduced to scales. *Inflorescences* terminal and/or axillary, generally cymose, often dichasial, the lateral axes often becoming monochasia, sometimes reduced to a single flower, rarely racemose, spicate or verticillate; bracts and bracteoles present or not. *Flowers* bisexual, rarely polygamous, usually 4- to 5-merous, usually actinomorphic, often showy; calyx gamosepalous, variously divided, generally imbricate, often persistent; corolla gamopetalous, usually contorted, generally tubular, the tube usually campanulate, salverform to infundibular, occasionally calcerate; stamens alternate with and the same number as the corolla lobes, inserted in the tube of the corolla, usually included, the filaments usually filiform, the anthers dorsifixed, often versatile, bilobate at the base, 2-celled, introrse, occasionally spirally twisting at maturity, longitudinally dehiscent, rarely poricidal; pollen[5] shed as monads or in tetrads; annular disc present or absent; pistil one, the ovary superior, generally unilocular with 2 protruding parietal placentae, occasionally bilocular with axile placentation, bicarpellate, the ovules numerous, anatropous, the style simple, varying in length, the stigma simple and usually capitate or bilamellate. *Fruit* a septicidal 2-valved capsule, membranous to coriaceous, rarely berry-like; seeds usually numerous, small, angulate, globose, sometimes ± compressed, sometimes winged, the testa variable, often appearing foveolate, reticulate or tuberculate; embryo tiny; endosperm usually copious.

The Gentianaceae are primarily a temperate family with approximately 75 genera distributed throughout the world. Twelve genera and 29 species are recognized as occurring in Panama. The genus *Nymphoides* is often included in the Gentianaceae in the subfamily Menyanthoideae, characterized by having

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[1] Assisted by National Science Foundation Grant GB-36202X (Thomas B. Croat, principal investigator).

[2] Assisted by National Science Foundation Grant GB-27713.

[3] The Cary Arboretum of the New York Botanical Garden, Box AB, Millbrook, New York 12545.

[4] Jardin Botanique National de Belgique, Domaine de Bouchout, B-1860 Meise, Belgium.

[5] Pollen descriptions by S. Nilsson, Palynologiska Laboratoriet, Wallenberglaboratoriet, Lilla Frescati, S-104 05 Stockholm 50, Sweden.

ANN. MISSOURI BOT. GARD. 62: 61–101. 1975.

the leaves alternate and the corolla lobes induplicate-valvate in bud. The genus occurs in Panama but has been treated as a separate family, the Menyanthaceae (Ann. Missouri Bot. Gard. 56: 29–32. 1969).

The diagnostic features of the pollen are taxonomically significant in defining generic limits and determining intergeneric relationships. Therefore, detailed pollen descriptions have been included in this treatment.

a. Plants with chlorophyll.
  b. Stigma undivided, capitate or clavate; pollen in monads.
    c. Flowers small, 5.5–8 mm long; corolla white.
      d. Leaves shorter than the internodes, narrowly linear; inflorescences loose ---------- 1. *Curtia*
      dd. Leaves considerably exceeding the internodes, narrowly ovate to ovate-elliptic; inflorescences of dense verticillate clusters ---------- 2. *Enicostema*
    cc. Flowers large, 2.8–5.4 cm long; corolla yellow to yellow-green, the lobes sometimes green ---------- 3. *Lisianthius*
  bb. Stigma bilamellate; pollen in monads or in tetrads.
    e. Petals calcarate (spurred) ---------- 4. *Halenia*
    ee. Petals without spur.
      f. Inflorescences spicate ---------- 5. *Coutoubea*
      ff. Inflorescences cymose or the flowers solitary.
        g. Anthers spirally twisting at maturity; flowers to 1.5 cm long ---------- 6. *Centaurium*
        gg. Anthers various, not twisting at maturity; flowers larger.
          h. Flowers 4-merous; calyx 4-carinate (keeled) to 4-alate dorsally ---------- 7. *Schultesia*
          hh. Flowers 5-merous.
            i. Flowers to 10 cm long; calyx lobes obtusely carinate (keeled) dorsally ---------- 8. *Symbolanthus*
            ii. Flowers to 5.5 cm long; calyx lobes not carinate (keeled).
              j. Leaves sessile; calyx 4–6 mm long; corolla tube gibbous, greenish-yellow ---------- 9. *Chelonanthus*
              jj. Leaves petiolate; calyx 13–18 mm long; corolla tube not gibbous, white or salmon-pink.
                k. Petioles to 2 cm long; flowers 3.3–4.0 cm long; corolla broadly infundibuliform, white; pollen in monads ---------- 10. *Macrocarpaea*
                kk. Petioles 3–5 mm long; flowers 5–5.5 cm long; corolla tube inflated for most of its length, constricted at base and apex, salmon-pink; pollen in tetrads ---------- 11. *Lagenanthus*
aa. Plants saprophytic, devoid of chlorophyll ---------- 12. *Voyria*

1. CURTIA

Curtia Cham. & Schlecht., Linnaea 1: 209. 1826.

Schuebleria Mart., Nov. Gen. Sp. Pl. Bras. 2: 113. 1827.

Herbs, annual, erect, slender, sparingly branched, the branches filiform, tetragonal. *Leaves* cauline, opposite, ternate or four per node, sessile, small, linear to lanceolate, rarely ovate to rotund. *Inflorescences* terminal, sometimes axillary, corymbiform to cymose, simple or compound dichasia or loosely paniculate. *Flowers* small, usually 5-merous, bracteate, white, pink, or yellow; calyx usually deeply lobed, the lobes narrow, acute, carinate; corolla tubular to infundibular, the tube often constricted slightly below the throat, the lobes small, contorted, obovate, ovate to lanceolate; stamens usually included, inserted at

or near the middle of the corolla tube, the filaments filiform, short, the anthers erect, oblong to ovate, bilobate at the base, the connective often conspicuous, terminating into a short mucro; pistil included, the ovary usually ovoid, 1-celled but appearing 2-celled by the strongly intruding placentae, the style filiform, short, the stigma capitate to short clavate. *Capsules* surrounded by the marcescent calyx, ovate to fusiform, septicidally 2-valvate; seeds numerous, small, irregular, foveolate. *Pollen grains* in monads, radially symmetrical, isopolar, subprolate, the amb ± rounded, 28–29 × 18–23 μ, 3-colporate, the colpi relatively long with tapering ± acute ends, the colpus membrane smooth, the ora lolongate, the diameter of apocolpia 7μ; exine 2μ thick; sexine thicker than nexine, finely reticulate or OL-pattern (*C. tenella*).

A genus of 8–10 species of small, often delicate herbs centered in northern and central South America but with at least one species in Central America.

1. **Curtia tenella** (Mart.) Cham., Linnaea 8: 13. 1833.—Fig. 1.

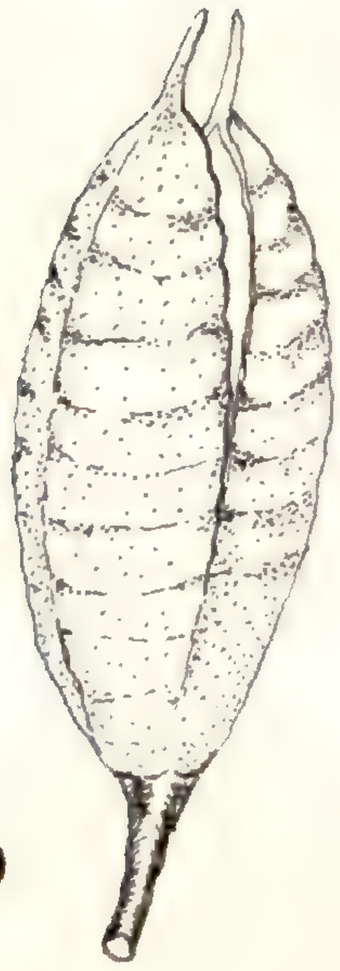
Schuebleria tenella Mart., Nov. Gen. Sp. Pl. Bras. 2: 117. 1826.

Herb, 5–32 cm in height; the stem slender, erect, rounded below, sharply 4-angular towards the apex, simple or sparingly branched above. *Leaves* sessile, narrowly linear, sometimes narrowly linear-obovate, acute to obtuse at the apex, shorter than the internodes, to 13 mm long and somewhat less than 1 mm wide. *Inflorescences* loose, composed of simple or compound, few-flowered dichasia, the terminal flower often replaced by several dichasia; pedicels 0.5–20 mm long; the bracts opposite, similar to the leaves but reduced in size. *Flowers* 5.5–6 mm long, (4–)5(–6)-merous; calyx 3–5 mm long, deeply 5-partite almost to the base, the lobes subulate, apically acuminate, dorsally carinate, scarious along the margins, ca. 0.5 mm wide at the base; corolla white, 5.5–7 mm long, the tube tubular, somewhat constricted below the throat, the lobes obovate, apically rounded (to acute?), 1.5–2 mm long and ca. 1.2–1.3 mm wide; stamens with the anthers subsessile or the filaments very short, inserted near the middle of the corolla tube, the anthers erect, narrowly oblong, ca. 0.6–0.7 mm long, 2-lobed at the base, each cell short-acuminate apically; ovary narrowly ovate, ca. 1.5 mm long, the style ca. 0.5 mm long, the stigma clavate, about as long as the style. *Capsule* equal to or usually somewhat shorter than the persistent calyx, oblong-ellipsoid, rostrate apically (persistent style), 3–3.5 mm long, septicidally 2-valvate, the valves rigid-chartaceous; seeds numerous, irregular, angular, ca. 0.25–0.3 mm long, the testa finely and minutely striate.

From Mexico to Brazil, in grasslands.

Known colloquially as "clavel de San Jacinto" on Taboga Island (cf. Standley, Contr. U.S. Natl. Herb. 27: 304. 1928).

CANAL ZONE: Ancon Hill, open grassy slopes, *Standley 25218, 26352* (both US). COCLÉ: Near Natá, 50 m, *Allen 832* (MO). Near Olá, 100–350 m, *Pittier 5039* (US). PANAMÁ: Near Pacora, 35 m, *Allen 994* (MO, US). Dry savannas, *Killip 3266* (MO, US). Sabanas, ca. 3 mi. E of Juan Días, *Cornman 2026* (US). Along road between Panama City and Chepo on savannas overlying lime outcrops, *Dodge et al. 16689* (MO). Hills NE of Hacienda La Joya, 50–300 m, *Dodge et al. 16890* (MO). San José Island, *Harlow 62* (GH, US); *Johnston 47, 877* (both GH). Taboga Island, dry hillsides, 200 ft, *Killip 3188* (US).



L. Mourrél,

2. ENICOSTEMA

Enicostema Blume, Bijdr. Fl. Nederl. Ind. 848. 1826.

Herbs, perennial, erect, rarely creeping, occasionally branched at the base, glabrous throughout; stems terete to angulate, frequently winged, often succulent. *Leaves* cauline, narrowly ovate to linear, sessile, often succulent. *Inflorescences* ± dense, axillary-clustered. *Flowers* small, 5-merous, sessile to subsessile; calyx narrowly campanulate to urceolate, carinate, the lobes narrowly ovate, fused at the base; corolla cylindrical becoming infundibular above, the lobes small, contorted, ± lax; stamens inserted at the middle of the corolla tube, the filaments filiform with a small double-hooded scale at the base, the anthers introrse, oblong, erect, apiculate; pistil usually included, the ovary 1-locular, the placenta slightly intruded, the style short, the stigma capitate. *Capsules* septicidally 2-valved; seeds tiny, the testa foveolate. *Chromosone number* $x = 19$. *Pollen grains* in monads, radially symmetrical, isopolar, suboblate to oblate spheroidal, the amb rounded-triangular, 24–26 × 26–31 μ, 3-colporate, the colpi short with acute or obtuse ends, the colpus membrane smooth, ora rounded to lolongate, well delimited, the diameter of apocolpia 20 μ; exine 2 μ thick; sexine as thick as nexine or thinner, finely reticulate or OL-pattern (*E. verticillatum*).

A small genus of 3 species in tropical regions of both hemispheres. One species, *Enicostema verticillatum*, is reported from Panama.

Literature:

Veldkamp, J. F. A synopsis of the genus *Enicostema* Bl., nom. cons. (Gentianaceae). Blumea 16: 133–136, *fig. 1.* 1968.

Raynal, A. Revision du genre *Enicostema* Blume (Gentianaceae). Adansonia, sér. 2. 9: 57–85, *pls. 1–10.* 1969.

1. **Enicostema verticillatum** (L.) Engl. *ex* Gilg *in* Engl. & Prantl, Nat. Pfl. 4(2): 67. June 1895; Engl., Pflanzenwelt Ostafr. C: 313. Aug 1895.—Fig. 2.

Gentiana verticillata L., Syst. Nat., ed. 10. 952. 1759.

Herb, 20–60 cm tall, unbranched or sparingly branched; stem terete at the base, becoming 4-angulate above, inconspicuously winged. *Leaves* considerably exceeding the internodes; the lamina narrowly ovate to ovate-elliptic, acuminate to subacute at the apex, gradually attenuate and amplexicaul at the base, chartaceous, with 3(–5) strongly ascending inconspicuous veins. *Flowers* in dense, axillary, verticillate clusters, usually 4–8 flowers per cluster, 6–8 mm long, white, sessile, bracteate, the bracts linear, 4–6 mm long; calyx 4–6 mm long, urceolate, the lobes subulate to narrowly linear-lanceolate, 2–4 mm long, flaring to recurved at the apex, the margins membranous; corolla 6–8 mm long, ± infundibular, white or yellow, the lobes ovate, narrowly acute at the apex, 1.5–2 mm

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Figure 1. *Curtia tenella* (Mart.) Cham.—A. Habit (× 9/10).—B. Flower (× 12).—C. Longitudinal section of flower (× 12).—D. Fruit (× 12). [A after *Allen 994* (MO). B–D after *Dodge et al. 16689* (MO).]

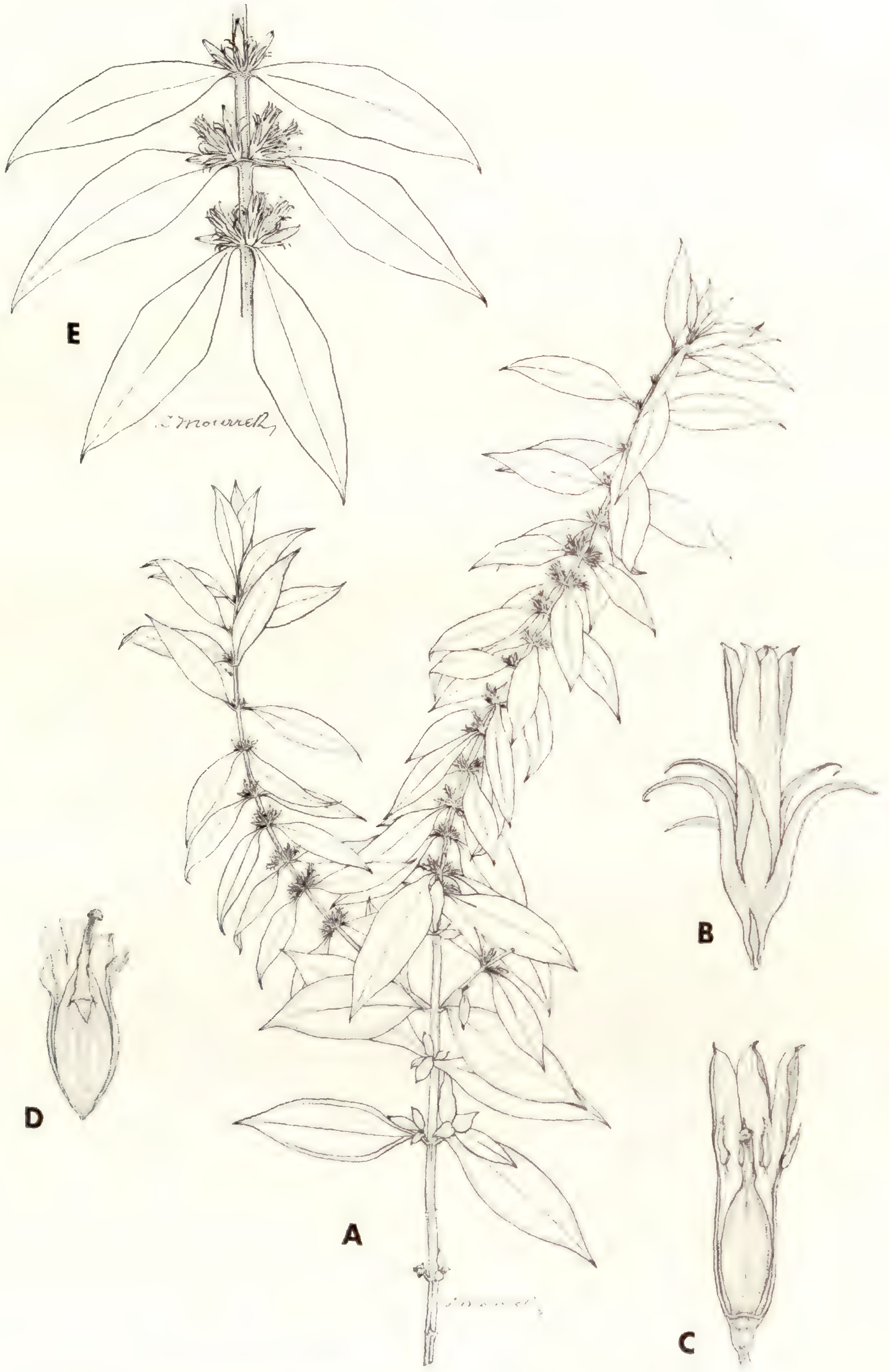

Figure 2. *Enicostema verticillatum* (L.) Engl. *ex* Gilg.—A. Habit (× ⅜).—B. Flower (× 5).—C. Longitudinal section of flower (× 5).—D. Fruit (× 5).—E. Nodal area showing

long and 0.5–1 mm broad at the base; stamens included, the filaments ca. 1 mm long, flattened, the anthers ca. 1.5 mm long, long-apiculate, bilobate at the base; pistil 2.6–2.8 mm long, ovary 1-locular, ellipsoid, 1.6–1.8 mm long, the cylindrical style ca. 1 mm long, the stigma ca. 0.5 mm in diameter. *Capsules* ellipsoid, 3.5–4 mm long, beaked (persistent style), surrounded by the marcescent calyx and corolla; seeds flattened.

This species is common in the Lesser Antilles, less abundant in the Greater Antilles and occurs on the Atlantic coast of Central America only in Panama. It appears to be restricted to beaches and coastal lowlands.

CANAL ZONE: Fort Sherman, *Stevens 254* (US). COLÓN: Near Viento Frío along beach, sea level, *Pittier 4140* (US). Garotte, about 10 km NE of Portobelo, *D'Arcy 4010* (MO). Miguel de la Borda, steep clay bank of sea coast, *Croat 10024* (MO). SAN BLAS: beach east of Puerto Obaldía, *Croat 16892* (MO).

3. LISIANTHIUS

Lisianthius P. Browne, Civ. Nat. Hist. Jamaica 157, *t.* 9. 1756. (See J. E. Dandy, Regnum Vegetabile 51: 61. 1967.)

Lisianthus L., Mant. Pl. 1: 6. 1767 (orthographic variant).
Leianthus Griseb., Gen. Sp. Gentianearum 196. 1838.

Herbs, perennial, rarely annual, occasionally suffrutescent, usually erect, often branching; stems terete to angulate, often becoming canaliculate above. *Leaves* sessile to petiolate; the petioles often amplexicaul; the lamina narrowly ovate, elliptic to obovate, submembranous to coriaceous. *Inflorescences* terminal and often axillary near the branch ends, few- to many-flowered, a thyrse, simple or compound dichasia, pedunculate. *Flowers* 5-merous, often showy, generally yellow, usually pedicellate, rarely sessile; calyx campanulate, lobed or parted to near the base, the lobes long-acuminate, rarely acute, often carinate; corolla contorted in aestivation, infundibular to salverform, usually constricted near the base, the lobes spreading to erect, equal, rarely unequal; stamens inserted on the lower part of the corolla tube, often unequal, the filaments filiform, included to exserted, the anthers introrse, oblong, versatile, usually apiculate; ovary 1-locular, usually appearing 2-locular (the placentae intruding and connected basally in the center of the ovary), the style filiform, often persistent, the stigma subcapitate to capitate. *Capsules* surrounded by the persistent and the marcescent corolla, frequently fusiform, septicidally 2-valvate; seeds commonly tuberculate or muricate. *Pollen grains* in monads, radially symmetrical, isopolar, (suboblate–) subprolate to prolate, the amb ± circular, 33–47 × 25–40 μ, 3-colporate (rarely 4-colporate), the colpi relatively long with tapering, ± acute ends, the colpus membrane smooth or granulose, the ora rounded to lolongate, the diameter of apocolpia 7–15 μ; exine 3–5 μ thick; sexine thicker than nexine, reticulate, heterobrochate, the lumina 0.5–7 μ in diameter, usually angular, the muri 0.5–1 μ wide supported by one row of bacules, of a pilum-like shape with ± pointed apices;

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densely clustered axillary flowers and the insertion of the petioles (× 5). [After *D'Arcy 4010* (MO).]

nexine smooth or granulose (*L. jefensis*, *L. peduncularis*, *L. seemannii*, *L. skinneri*).

A neotropical genus of 14–16 species in Mexico, Central America, the West Indies and reaching into northern South America. Four species are known from Panama, 2 of which are endemic.

Literature:

Nilsson, S. Pollen morphological contributions to the taxonomy of *Lisianthus* L. s. lat. (Gentianaceae). Svensk. Bot. Tidskr. 64: 1–43. 1970.

Perkins, J. Monographische Ubersicht der Orten der Gattung *Lisianthus* (Gentianaceae). Bot. Jahrb. (Syst.) 31: 489–494. 1902.

Weaver, R. E., Jr. A revision of the neotropical genus *Lisianthius* (Gentianaceae). Jour. Arnold Arbor. 53: 76–100, 234–311. 1972.

a. Corolla infundibular, the tube not inflated, broadest at the apex, the lobes 1.2–1.5 cm long, cuspidate-acuminate at the apex ..... 1. *L. seemannii*
aa. Corolla tubular, the tube distinctly inflated, broadest near the middle, the lobes 2–8 mm long, acute to acuminate at the apex.
  b. Leaves subcoriaceous; flowers 2.8–3.2 cm long ..... 2. *L. jefensis*
  bb. Leaves membranous to chartaceous; flowers 3.5–5.4 cm long.
    c. Corolla lobes 6–8 mm long; anthers 4–5 mm long; flowers 4.2–5.4 cm long ..... 3. *L. peduncularis*
    cc. Corolla lobes 2–3.5 mm long; anthers 2–3 mm long; flowers 3.5–4.6 cm long ..... 4. *L. skinneri*

1. **Lisianthius seemannii** (Griseb.) O. Kuntze, Rev. Gen. Pl. 2: 429. 1891.—FIG. 3E–H.

Leianthus seemannii Griseb. *in* Seem., Bot. Voy. Herald 170. 1854.
Lisianthus seemannii (Griseb.) Perkins, Bot. Jahrb. (Syst.) 31: 491. 1902.
L. corymbosus Perkins, Bot. Jahrb. (Syst.) 31: 491. 1902.

Herb or shrub, 0.2–2.0 m tall, the stems terete, green. *Leaves* distinctly petiolate basally, the upper ones nearly sessile, the petioles amplexicaul; lamina ovate, attenuate into the petiole to rounded and decurrent at the base, long-acuminate apically, to 12 cm long and 4.8 cm wide, thin-chartaceous, the costa slightly prominent and the lateral veins prominulous beneath. *Inflorescences* terminal and axillary, dense, borne in simple or compound dichasia; the peduncles short to elongate and attaining 6.5 cm, angulate; the pedicels short, 2–5 mm long; the bracts similar to the leaves but much reduced. *Flowers* 3.5–4.5 cm long; calyx 11–13 mm long, the lobes united only ca. 2 mm at the base, narrowly ovate, conspicuously carinate dorsally, sharply acuminate at the apex, ca. 2.5–3 mm wide, the margins scarious; corolla pale yellow to yellow, 3.5–4.5 cm long, the tube narrowly infundibuliform, ± constricted at the apex of the calyx, the lobes ovate to narrowly ovate, long-cuspidate-acuminate, 1.2–1.5 cm long and 0.4–0.6 cm wide, erect; stamens exserted, the filaments inserted on the lower part of

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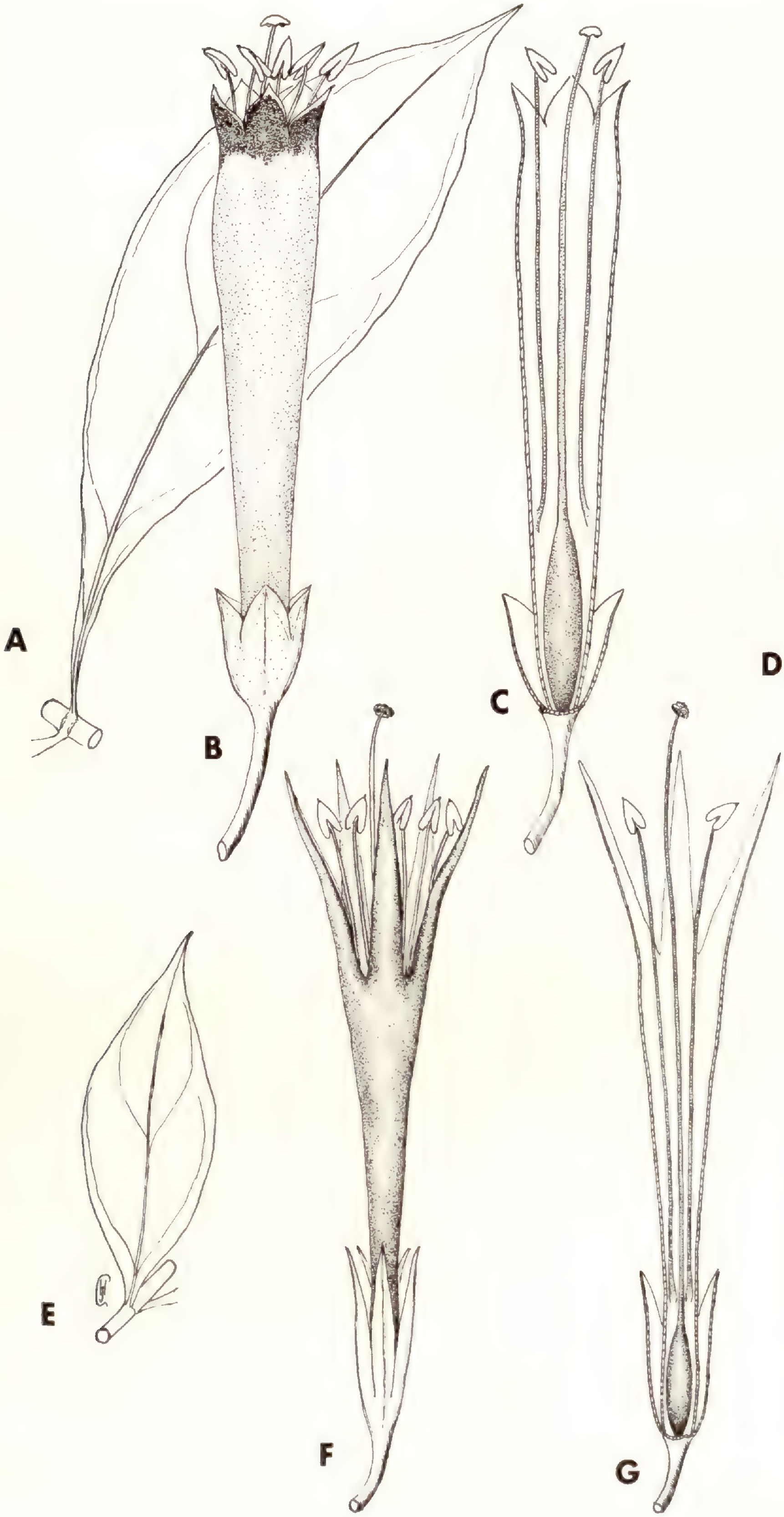
FIGURE 3. *Lisianthius*.—A–D. *L. skinneri* (Hemsley) O. Kuntze.—A. Leaf (× ½).—B. Flower (× 2).—C. Longitudinal section of flower (× 2).—D. Fruit (× 2).—E–H *L. seemanii* (Griseb.) O. Kuntze.—E. Leaf (× ½).—F. Flower (× 2).—G. Longitudinal section of flower (× 2).—H. Fruit (× 2). [A–D after *Allen & Allen 5104* (MO). E–H after *Burch et al. 1324* (MO).]


A
B
C
D
E
F
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H

the corolla tube, ca. 5–7 mm above the base, filiform, 2.5–3 cm long, the anthers ca. 2.1–2.2 mm long, the uncinate apical mucro inconspicuous or wanting; ovary fusiform, 5–6 mm long, ca. 0.5–0.6 mm in diameter, the style short- to long-exserted, the stigma capitate. *Capsule* fusiform, to 1 cm long; seeds irregular, ca. 0.5 mm long.

Costa Rica, Panama and Colombia.

CHIRIQUÍ: Between Hato del Jobo and Cerro Vaca, 700–1000 m, *Pittier 5292* (NY, US). COCLÉ: Near El Valle de Antón, 800–1000 m, *Allen 121, 783* (both MO); *Harvey 5168* (F). 3.5 km SE of El Valle de Antón, *Weaver et al. 2248* (MO). Hills S of El Valle de Antón, 600–800 m, *Allen 2850* (F, MO), *4210* (MO). Mountains beyond La Pintada, 400–600 m, *Hunter & Allen 621* (MO). El Valle de Antón, 330–680 m, edge of cloud forest and roadside, *Lewis et al. 2582* (MO). Llano Bonito, N of Las Margaritas, 400–500 m, *Siebert 530* (MO). Bismark above Penonomé, *Williams 259* (NY), *629* (US). DARIÉN: Piñas, *Seeman 1064* (K, holotype, not seen; F, MO, photo). Near Piñas, *Duke 10637* (MO). HERRERA: Between Las Minas and Pesé, roadside in hills, 300–400 m, *Burch et al. 1324* (MO); *Duke 12321* (MO). 12.5 mi. S of Ocú, 400 m, secondary woods on hillside, infrequent, *Lewis et al. 1643* (MO). Near Las Minas, La Peña, rain forest type, *Stern et al. 1779* (MO). 10 mi. S of Ocú, road bank, *Tyson et al. 2876* (MO). VERAGUAS: Isla de Coiba (Colonia Penal), *Dwyer 1650* (MO).

2. **Lisianthius jefensis** A. Robyns & Elias, Ann. Missouri Bot. Gard. 55: 60, *fig. 1.* 1968. (As "*Lisianthus*".)

Herb or shrub, 1–2.4 m tall; the stems green, terete. *Leaves* petiolate; the petioles amplexicaul; the blade narrowly obovate, long-attenuate into the petiole and decurrent at the base, apically acuminate, to 12 cm long and 4 cm wide, subcoriaceous, the costa prominent beneath. *Inflorescences* terminal and axillary, open, composed of simple or compound, few-flowered dichasia; the peduncles to 4.5 cm long; the pedicels 1–2.5 cm long; the bracts opposite, 2–5 mm long. *Flowers* 2.8–3.2 cm long; calyx tubular, 7–9.5 mm long, the lobes narrowly ovate, slightly carinate, long-acuminate apically, 4–6.5 cm long and ca. 2–2.5 mm wide, ± scarious along the margins; corolla bright yellow, 2.8–3.2 cm long, tubular, the lower ⅓ constricted, the lobes greenish-yellow, erect, triangular, acuminate, 4–5.5 mm long and ca. 3 mm wide; stamens included or short-exserted, the filaments filiform, inserted on the corolla tube ca. ⅓ way from the base, 19–24 mm long, the anthers ca. 3.5–4 mm long, sagittate at the base, mucronate at the apex, the mucro curved and ca. 0.3–0.4 mm long; ovary narrowly ovate, slightly and obtusely 4-angulate at the base, 6–7 mm long and ca. 1.5–2 mm in diameter, the style equalling the corolla tube to long-exserted, the stigma capitate, ca. 1 mm in diameter. *Capsule* fusiform, beaked (persistent style base), to 12 mm long.

Endemic to Panama, found only on Cerro Jefe, Panamá Province.

PANAMÁ: Region of summit of Cerro Jefe, 900 m, *Correa & Dressler 1154* (MO). 10 km above Goofy Lake on road to Cerro Jefe, *Weaver & Foster 1481* (MO, DUKE). Cerro Jefe, 2.5 mi. beyond Finca Indio, *Gentry 2115, 6771* (both MO). Cerro Jefe, *Duke 9413* (MO); *Busey 798* (MO); 10–13 mi. S of Goofy Lake, *Duke 8010* (MO); summit, secondary cloud forest, *Dwyer et al. 5035* (MO); *Weaver & Wilbur 2241* (MO); 950 m, roadside thicket, *Dwyer & Hayden 8087* (MO, US); cloud forest, *Elias & Hayden 1798* (MO, holotype; UC, isotype); summit and forest along road beyond summit, *Hayden 1008* (COL, DUKE, MO, US); down slope from summit, *Kirkbride & Crebbs 16* (MO); top, very common, *Tyson et al. 4438* (MO); slopes of Cerro Jefe, *Weaver & Wilbur 2250, Weaver & Wilbur 2243* (both MO).

3. **Lisianthius peduncularis** L. O. Wms., Fieldiana: Bot. 31: 408, *fig 1.* 1968. (As "*Lisianthus*".)

Large *herb* or shrub to 3 m tall; the stems terete, becoming angulate and canaliculate near the apex. *Leaves* petiolate; the petiole 1–2 cm long, amplexicaul; lamina elliptic to obovate, basally cuneate, apically acuminate to 15 cm long and 6 cm wide, membranous to thin-chartaceous with 2–4 pairs of ascending lateral veins, the costa prominent beneath, glabrous. *Inflorescences* terminal and axillary, open, borne in simple or compound, few-flowered dichasia; the peduncles to 4 cm long; the pedicels 0.8–1.8 cm long; the bracts opposite, to 3 mm long. *Flowers* 4.2–5.4 cm long; calyx tubular, 6–10 mm long, the lobes lanceolate, carinate, long-acuminate at the apex, 4–7 mm long; corolla 4.2–6 cm long, tubular, the tube bright yellow, the lower ¼ constricted, the lobes green, ovate, acuminate, 6–8 mm long and ca. 3–4 mm wide at the base, erect; stamens equalling the lobes or shortly exserted, the filaments filiform, inserted on the corolla tube ca. ¼ from the base, 3.6–4.8 cm long, the anthers 4–5 mm long, the apical mucro to 0.5 mm long, curved; ovary narrowly ovoid, inconspicuously 4-angulate at the base, 8–12 mm long, ca. 2–3 mm in diameter, the style included to shortly exserted, the stigma capitate. *Capsule* fusiform, 12–14 mm long and 3–4 mm in diameter, with a beak to 4 mm long; seeds irregular.

Known only from central Panama.

COCLÉ: El Valle de Antón, *Allen 3410* (MO, holotype). Near La Mesa N of El Valle de Antón, *Allen 2369* (MO). Near El Valle de Antón, *Allen 1793* (MO, NY). Cerro Pajita, hills N of El Valle de Antón, *Allen 4187* (MO). Summit of Cerro Pilón, *Croat 22945* (MO). Along trail to La Mesa about 4.5 miles beyond El Valle de Antón, *Wilbur & Luteyn 11696* (MO).

4. **Lisianthius skinneri** (Hemsley) O. Kuntze, Rev. Gen. Pl. 2: 429. 1891.—FIG. 3A–D.

Leianthus skinneri Hemsley, Biol. Centr. Amer. 2: 345. 1882.
Lisianthus arcuatus Perkins, Bot. Jahrb. (Syst.) 31: 492. 1902.
L. skinneri (Hemsley) Perkins, Bot. Jahrb. (Syst.) 31: 492. 1902.
L. scopulinus A. Robyns & Elias, Ann. Missouri Bot. Gard. 55: 62, *fig. 2.* 1968.

Herb or shrub, 1.5–3 m tall; the stems terete, erect, light green. *Leaves* petiolate; the petiole amplexicaul; lamina obovate to obovate-elliptic, long-attenuate into the petiole, acuminate apically, mucronate, 6–24 cm long and to 7.6 cm wide, chartaceous to submembranous, the costa prominent, lateral veins in 2–3 pairs, strongly ascending. *Inflorescences* terminal and axillary, composed of 1–3 laxly-flowered, simple or compound dichasia; the peduncles 1.4–6 cm long, terete, the pedicels 0.8–2.7 cm long; the bracts opposite, lanceolate to sublinear, 2–3 mm long. *Flowers* 3.5–4.1 cm long; calyx 4–7 mm long, cupular, the lobes 2–3 mm long, ovate, carinate dorsally, narrowly acuminate and appearing long-mucronate at the apex, the margins membranous; corolla 3.5–4.1 cm long, tubular, the tube bright yellow, constricted at the base, expanding slightly toward the apex, the lobes ovate, 2.5–3.5 mm long, erect, dark green, short-acuminate at the apex; stamens exserted, the filaments inserted ca. ⅓ from the base of the corolla, filiform, 2.5–3.2 cm long, the anthers ca. 2.5 mm long, bilobate at the

base, inconspicuously mucronate apically; pistil 3.6–4.6 cm long, exserted, ovary narrowly ovate, 1–1.2 cm long, ca. 3 mm in diameter, the style exserted, the stigma capitate. *Capsule* fusiform, 1.5–1.9 cm long, beaked by the persistent style, the beak to 1.2 cm long; seeds irregular, ca. 0.5 mm long.

Known in Guatemala, Honduras, Costa Rica, and southward to Panama.

CANAL ZONE: W of Limón Bay, Gatun Locks and Gatun Lake, *Johnston 1502* (MO). Forest along telephone cable trail between splice S16 and S49, Río Indio, *Steyermark & Allen 17427* (MO). COCLÉ: Near La Mesa, El Valle de Antón, *Allen 2369* (MO). COLÓN: Summit of Cerro Santa Rita, *Allen & Allen 5104* (MO). María Chiquita, E of Río Piedras toward Portobelo, *Dwyer & Kirkbride 771* (COL, DUKE, K, MO, US). 5–7 mi. to SE of Portobelo, *Weaver & Wilbur 2249* (MO). West of Portobelo, *D'Arcy & D'Arcy 6698* (MO). PANAMÁ: Slopes of Cerro Jefe, *Weaver & Wilbur 2244* (MO). Along road from Cerro Azul to Cerro Jefe, *Tyson 5320* (MO). Slopes of Cerro Jefe beyond Cerro Azul, about 5.5 mi. on the road to La Eneida, *Wilbur & Teeri 13606* (MO). Altos del Río Pacora, *Lewis et al. 2314* (MO). VERAGUAS: Mouth of Río Concepción, *Lewis et al. 2799* (MO, DUKE, F, K, type of *L. scopulinus*).

4. HALENIA

Halenia Borckh. *in* Roemer, Ark. Bot. 1: 25. 1796.

Herbs, annual, biennial or perennial. *Leaves* sessile or petiolate, usually 3–5-veined, membranous to fleshy. *Inflorescence* terminal or axillary, subumbellate, rarely a raceme or spicate cyme. *Flowers* with the calyx 4-parted, foliaceous, the lobes linear, narrowly ovate, ovate or spathulate, usually papillate and bearing a small squamella at the base; corolla 4-parted, white, yellow, green or purple, campanulate, marcescent, the lobes dextrorsely convolute, elliptic to ovate, obtuse to acute, occasionally apiculate, entire to erose, often auriculate and papillate, prolonged at the base into usually short, retrorse spurs; stamens 4, included, adnate to the corolla tube, the filaments linear or ± dilated, the anthers ovate, oblong, or subtriangular, versatile; pistil included, the ovary sessile, the stigma bilobate. *Fruit* a compressed capsule, narrowly ovate to ovate, often subfalcate, septicidally dehiscent, surrounded by the marcescent calyx and corolla; seeds globose or ± flattened, brown to greenish tan, the testa granular or reticulate. *Pollen grains* in monads, radially symmetrical, isopolar, subprolate to prolate, the amb ± triangular, 40 × 28 μ, 3-colporate, the colpi relatively long with tapering ± acute ends, the colpus membrane smooth, ora rounded, relatively small, diameter of apocolpia 10 μ; exine 2 μ thick; sexine as thick as nexine, smooth or OL-pattern (*H. woodsoniana*).

A genus of ca. 70 species extending from Labrador and Newfoundland southward to South America. Three species are known from Panama.

Literature:

Allen, C. K. A monograph of the American species of the genus *Halenia*. Ann. Missouri Bot. Gard. 20: 119–222, 7 *fig.*, *pl.* 8–12. 1933.

a. Cauline leaves elliptic to ovate-elliptic, conspicuously apiculate; spur of the corolla more than ½ as long as the corolla ..... 1. *H. euryphylla*
aa. Cauline leaves linear-ovate to narrowly ovate, apically acute; spur of the corolla less than ½ as long as the corolla.
b. Leaves basal and cauline, the basal leaves often in a dense rosette; stems to 20 cm tall; inflorescences ± compact, flowers often congested ..... 2. *H. rhyacophila*

FIGURE 4. *Halenia euryphylla* C. Allen.—A. Habit (× ½).—B. Flower (× 4).—C. Longitudinal section of flower (× 4).—D. Fruit (× 3). [A, D after *Allen 4900* (MO). B–C after *Woodson & Schery 362* (MO).]

bb. Leaves cauline, more or less crowded near the base, no basal rosette; stems to 70 cm tall; inflorescences spreading, loosely flowered ..... 3. *H. woodsoniana*

1. **Halenia euryphylla** C. Allen, Ann. Missouri Bot. Gard. 28: 459. 1941.—FIG. 4.

Herb, perennial (?), to ca. 50 cm tall; stems simply branched, procumbent, terete, faintly striate. *Leaves* elliptic to ovate-elliptic; the petiole to 2.5 cm long, often evanescent into the basal portion of the lamina, flattened; the lamina 2–6 cm long and 1–2.9 cm broad, conspicuously apiculate, the apiculum 1–1.5 mm long, basally attenuate, membranous, trinervate, the veins conspicuously anastomosing. *Inflorescences* terminal, rarely axillary, the cymes lax, few-flowered; the pedicels 1–2 cm long, spreading to subascending. *Flowers* greenish-yellow; calyx lobes narrowly obovate, apiculate at the apex, 7–10 mm long and 2–2.5 mm broad, trinervate, minutely papillose; corolla lobes obovate to elliptic, obtuse and erose at the apex, 9–11 mm long and 4–5 mm broad near the apex, the spur 5–8 mm long, spreading to slightly descending, 0.5–1 mm in diameter; stamens 4.4–5.2 mm long, the filaments 3–3.5 mm long, linear, flattened, the anthers 1.4–1.7 mm long, the thecae free and slightly spreading at the base; pistil 5–6 mm long, the ovary ellipsoid, 3–4 mm long, the style evanescent from the ovary, the stigmatic lobes 0.5 mm long, truncate at the apex. *Capsules* ellipsoid, 1.2–1.5 cm long, ± lustrous, the style and stigma persisting; seeds ellipsoid, 1–1.3 mm long, lustrous, smooth, light tan.

Known only from Cerro Copete, 2300–3000 m, in the Province of Chiriquí in Panama.

CHIRIQUÍ: Casita Alta to Cerro Copete, *Woodson & Schery 362* (MO, holotype; GH, isotype). Summit and SW face of Cerro Copete, *Allen 4900* (BR, MO).

2. **Halenia rhyacophila** C. Allen, Ann. Missouri Bot. Gard. 20: 168. 1933.

Herb, perennial, to 18 cm tall (Panama); the stems single or several-branched at the base, terete, inconspicuously winged, the internodes very short. *Leaves* basal and cauline, the basal leaves often in a dense rosette, narrowly deltoid, apically acute to short-apiculate, basally long-attenuate, sessile to subsessile, 3.5–5.2 cm long and 0.3–0.5 cm broad, trinervate, ± undulate, the cauline leaves linear-ovate, acute at the apex, long-attenuate into a short petiole, 1–3.5 cm long and 2–3 mm broad, trinervate. *Inflorescences* terminal or axillary, appearing cymose or racemose, ± compact, several- to many-flowered, the flowers often appearing congested; the pedicel 1–2.5 cm long, strongly ascending. *Flowers* white; calyx lobes narrowly ovate to narrowly oblong-ovate, acute at the apex, 5–7 mm long and 1–1.5 mm broad, trinervate, ± papillate; corolla lobes ovate to elliptic, obtuse, acute to short acuminate at the apex, the margin minutely erose, 5–10 mm long and 3.5–5 mm broad, ± papillate, the spurs 2.5–4 mm long, descending to strongly descending, 0.3–0.7 mm in diameter; stamens 4–4.7 mm long, the filaments 2.5–3 mm long, linear, flattened, the anthers 1.5–1.7 mm long, the thecae free and slightly spreading at the base; pistil ca. 5.2 mm long, the ovary ellipsoid, ca. 3 mm long, evanescing into the style, the stigmatic lobes ca. 0.5 mm long, truncate at the apex. *Capsules* ellipsoid, 10–12 mm long, ± lustrous,

the style and stigma often persisting; seeds ellipsoid, 1.2–1.5 mm long, smooth, brown.

Common at higher altitudes in Costa Rica and extending into the Province of Chiriquí in Panama.

CHIRIQUÍ: Cerro Pando, valley of the upper Río Chiriquí Viejo, *White 7* (MO).

3. **Halenia woodsoniana** C. Allen, Ann. Missouri Bot. Gard. 26: 298. 1939.

Herb, perennial (?), 40–70 cm tall; the stems single or sparingly branched at the base, ± procumbent, terete, inconspicuously winged, the internodes 1–7.6 cm long. *Leaves* cauline, crowded near the base, narrowly ovate to linear-ovate, acuminate at the apex, slightly attenuate at the base, sessile, 1.8–6.2 cm long, 0.3–0.8 cm broad, trinervate, the costa prominent beneath. *Inflorescences* terminal or supra-axillary, cymose, spreading, few-flowered; the pedicels 2–5.8 cm long, strongly ascending. *Flowers* greenish to pale greenish-yellow; calyx lobes narrowly ovate, acuminate at the apex, 8–11 mm long and 1.5–2.5 mm broad near the base, obscurely trinervate; corolla lobes ovate to elliptic, obtuse to acute, 8–12 mm long and 4–6 mm broad, very lightly erose, the spurs 3–4 mm long, horizontal to slightly descending, 0.7–1 mm in diameter; stamens 4–5 mm long, the filaments 3–3.2 mm long, linear, flattened, the anthers 1.2–1.5 mm long, the thecae free and spreading at the base; pistil 5.8–6 mm long, the ovary ellipsoid, ca. 3.5 mm long, evanescing into the style, the stigmatic lobes ca. 0.5 mm long. *Capsules* ovoid to ellipsoid, 1.4–1.8 cm long, lustrous; seeds ellipsoid, 1–1.2 mm long, smooth, brown.

Endemic to Panama.

CHIRIQUÍ: Volcán de Chiriquí, Loma Larga to summit, ca. 2500–3380 m, *Woodson et al. 1052* (MO, holotype; GH, NY, isotypes). Potrero Muleto, Boquete, 3460 m, *Davidson 994* (F, GH, MO).

5. COUTOUBEA

Coutoubea Aubl., Hist. Pl. Guiane Fr. 1: 72. 1775.

Herbs, rarely trailing, erect, annual or perennial (?), simple to branched, the branches usually strongly ascending, terete. *Leaves* cauline, opposite or rarely ternate, the lamina lanceolate, oblong-lanceolate to oblanceolate, sessile, becoming amplexicaul, acute to long-acute at the apex, membranous to coriaceous. *Inflorescences* terminal or axillary, spicate or racemose, dense to long-interrupted, many-flowered. *Flowers* 4(–5)-merous, small, sessile to shortly pedicellate; calyx campanulate, deeply lobed, the lobes lanceolate-ovate, scarious-marginate; corolla white, often tinged with blue or purple, the tube short-cylindric, the lobes lanceolate to lanceolate-ovate, spreading; stamens inserted near the apex of the tube, the filaments filiform, spreading at the base, the anthers oblong, erect, bifid; ovary narrowly ovoid, ovary 1-locular, the placenta strongly intruding, the style filiform, the stigma bilamellate, the lobes oblong, flattened. *Capsules* surrounded by the marcescent calyx and/or corolla, ovoid-ellipsoid, septicidally 2-valvate; seeds small, numerous, globose, foveolate, appearing reticulate. *Pollen grains* united in tetrahedral tetrads, 55–64 μ; single grains 3-

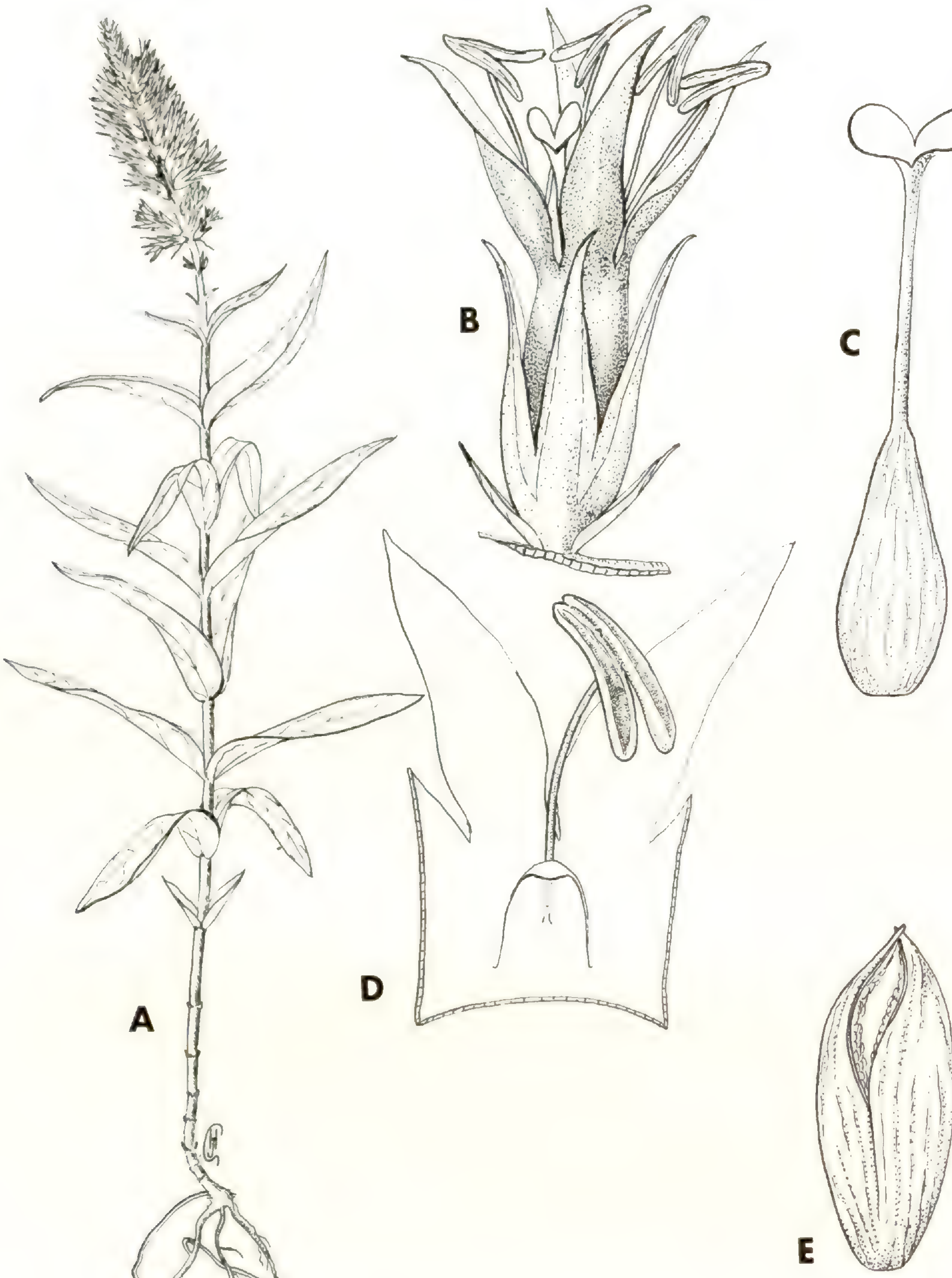


FIGURE 5. *Coutoubea spicata* Aubl.—A. Habit (× 3/5).—B. Flower (× 6).—C. Gynoecium (× 8⅖).—D. Interior portion of corolla showing stamen (× 8⅖).—E. Fruit (× 6). [After *Lewis et al. 1834* (MO).]

colporate (3-colpate, 3-porate), the concurrent colpi of two contiguous grains ca. 18 × 16 μ, the ora usually not confluent, the colpus membrane granulose, the diameter of apocolpia 22–25 μ; exine 4–6 μ thick at the distal poles, decreasing in thickness towards equator; sexine thicker than nexine, reticulate, heterobrochate, the lumina (0.5–)1–5 μ in diameter, the muri 0.5–1 μ wide; nexine usually smooth (*Coutoubea spicata*).

A small genus of perhaps 5 species primarily of South America, but with one species extending into Central America to extreme southern Mexico.

1. **Coutoubea spicata** Aubl., Hist. Pl. Guiane Fr. 1: 72, *t. 27*. 1775.—Fig. 5.

Exacum spicatum (Aubl.) Vahl, Symb. Bot. 3: 17. 1794.
Coutoubea densiflora Mart., Nov. Gen. Sp. Pl. 2: 112, *t. 185*. 1826.

Herb, annual to 1.2 m tall; the stem erect, simple or sparsely branched, subterete (obtusely tetragonous). *Leaves* opposite-decussate; blade narrowly ovate-triangular or narrowly oblong-ovate, rounded at the base, long and sharply acute at the apex, to 11 cm long and 3.5 cm wide, spreading, the costa somewhat prominent beneath, the basal leaves elliptic to subobovate and rounded at the apex. *Inflorescences* terminal or axillary, spicate, the spikes elongated, to 20 cm long, densely flowered. *Flowers* decussate, the bracts to 4.5 mm long, the bracteoles 2–2.5 mm long; calyx 6–7 mm long, 4-lobed, the lobes unequal, narrowly triangular-acuminate, carinate, 3.5–4.5 mm long; corolla 11.5–13.5 mm long, white or greenish-white, the tube cylindrical, 5–6.6 mm long, the lobes patent, ovate, acute at the apex, 6–7 mm long and 2.8–3 mm wide; stamens with the filaments ca. 2.5 mm long, the anthers sagittate, obtuse, 3–3.2 mm long; ovary narrowly ovate, ca. 4 mm long and 1.5 mm in diameter, the style ca. 3.5 mm long, enlarged towards the apex, the stigma lobes erect, at least 1 mm long. *Capsule* narrowly ovate, acuminate, about as long as the calyx; seeds globose, ca. 0.3 mm long, the testa reticulate.

This common species occurs from northern South America through Central America to Chiapas, Mexico.

CANAL ZONE: Albrook Air Force Base on Beacon Hill, *Tyson 2037* (MO). Ancon Hill, *Greenman & Greenman 5083* (MO); *R. S. Williams 30* (NY). Around Culebra, *Pittier 2234* (NY). NW shore of Gatun Lake, ca. 4 mi. S of Río Chagres, *Lewis et al. 1834* (MO). In government forest along Las Cruces Trail, 75 m, *Hunter & Allen 701* (MO). Fort Kobbe, *Duke 3965* (MO). Along powerline between Miraflores and Panamá, *Blume 2062* (MO). Paraíso, *Dwyer 7157* (MO). Sabanas along Río Azote Caballo, *Dodge et al. 16836* (MO). HERRERA: 10 mi. S of Ocú, *Tyson et al. 2845* (MO). Roadsides in hills between Las Minas and Pesé, *Burch et al. 1339* (GH, MO). PANAMÁ: Along road toward top of Cerro Campana, bald savanna-like area, *Duke 5957* (GH, MO). Grassland near La Chorrera, Río Bernadino between Arraisán and La Chorrera, *Dodge et al. 16741* (MO). Pan Am Highway at Río Mamonía, 4 mi. beyond Chepo, *Duke 5568* (MO). Along road between Panamá and Chepo, *Dodge et al. 16656* (MO). Low thick scrub along Río Tocumen, N of Chepo, *Hunter & Allen 223* (MO). Isla del Rey, *Duke 9501* (MO). Isla Taboga, *Duke 5902* (MO); *Miller, Jr. 1853* (MO); *Woodson et al. 1460* (MO). SAN BLAS: Mainland point opposite Isla Mosquito, *Duke 8974* (MO). VERAGUAS: Trail between Cañazas and foot of Cordillera Central, headwater of Río Cañazas, 300–600 m, *Allen 178* (MO). Ca. 5 mi. NE of La Mesa, *Blume & Tyson 660* (MO). Hills W of Soná, ca. 500 m, *Allen 1053* (MO). WITHOUT PROVINCE: *Grisebach s.n.* (MO).

6. CENTAURIUM

Centaurium Hill, Brit. Herb. 62. 1756.

Erythraea Neck., Elem. Bot. 2: 10. 1790.

Herbs, annual, biennial, or perennial, often with a basal rosette of leaves; stems erect to procumbent at the base, terete to angulate, often branched. *Leaves* sessile to subsessile, occasionally amplexicaul. *Inflorescences* of loose cymes, corymbiform or capituliform with a usually sessile central flower, or the cymes unpaired and spicate, or in reduced dichasia, or the flowers solitary. *Flowers* with 2 opposite bracts, 4- to 6-merous; calyx tubular at the base, the lobes carinate; corolla contorted, dextrorse, usually pink, sometimes yellow or white, the tube cylindrical, shorter to longer than the lobes, the lobes spreading to ascending at anthesis; stamens with the filaments filiform, inserted on the corolla tube, the anthers introrse, subbasifixed and spirally twisting at maturity; ovary sessile, elongate, 1-celled, the placentae often intruded, the style filiform, exserted, the stigmas bilamellate. *Capsules* elongate, surrounded by the marcescent calyx and corolla, septicidally 2-valvate; seeds minute, variously shaped, the testa finely reticulate. *Pollen grains* in monads, radially symmetrical, isopolar, subprolate to prolate, the amb rounded-triangular, 24–29 × 18–23 μ, 3-colporate, the colpi relatively long with tapering, ± acute ends, the colpus membrane smooth or finely granular, the ora usually lolongate with lateral extensions, the diameter of apocolpia 6–7 μ; exine 3 μ thick; sexine thicker than nexine, striate, striate-reticulate, rarely reticulate, the lirae (muri) 0.6–0.8 μ wide, parallel or not, crisscrossed (*C. quitense*, *C. strictum*).

A genus of approximately 40 species in temperate and tropical regions of the Old and New World with 2 species reported from Panama.

a. Calyx lobes equal to the tube; lower leaves narrowly obovate; flowers 8–15 mm long; corolla lobes 5–6 mm long; stigma shallowly bilobate ..... 1. *C. strictum*
aa. Calyx lobes longer than the tube; lower leaves narrowly ovate to elliptic; flowers 6–9 mm long, corolla lobes 2–4 mm long; stigma distinctly bilobate ..... 2. *C. quitense*

1. **Centaurium strictum** (Schiede) Druce, Bot. Soc. Exch. Club Brit. Isl. Rep. (for 1916) 4: 614. 1917.—FIG. 6D–F.

Erythraea stricta Schiede, Periód. Acad. Med. Mégico 1: 14. 1836 (in Schlecht., Bot. Zeit. 13: 918. 1855).

Herb 7.5–50 cm tall; stems erect, sparingly branched, the branches strongly ascending, 4-angular, slightly winged. *Leaves* cauline, the lower ones oblanceolate, the upper ones narrowly ovate to narrowly ovate-linear, acute to subobtuse at the apex, ± attenuate at the base, 0.8–2.1 cm long and 1–4.5 mm broad, thin-chartaceous, 3-veined, the veins basally connate and inconspicuous. *Inflorescences* terminal and axillary, solitary in the axils or in simple, few-flowered dichasia; the peduncles angular, slightly winged, 2.5–4 cm long; the pedicels 0.5–1 cm long. *Flowers* usually 5-merous, pink, 0.8–1.5 cm long; calyx campanulate, 5–6 mm long, the lobes conspicuously carinate, 2.5–3 mm long; corolla 8–15 mm long, the tube ellipsoid, slightly constricted below the lobes, the lobes 5–6 mm long, ovate, acute at the apex, slightly spreading; stamens included, 1.2–1.7 mm long,

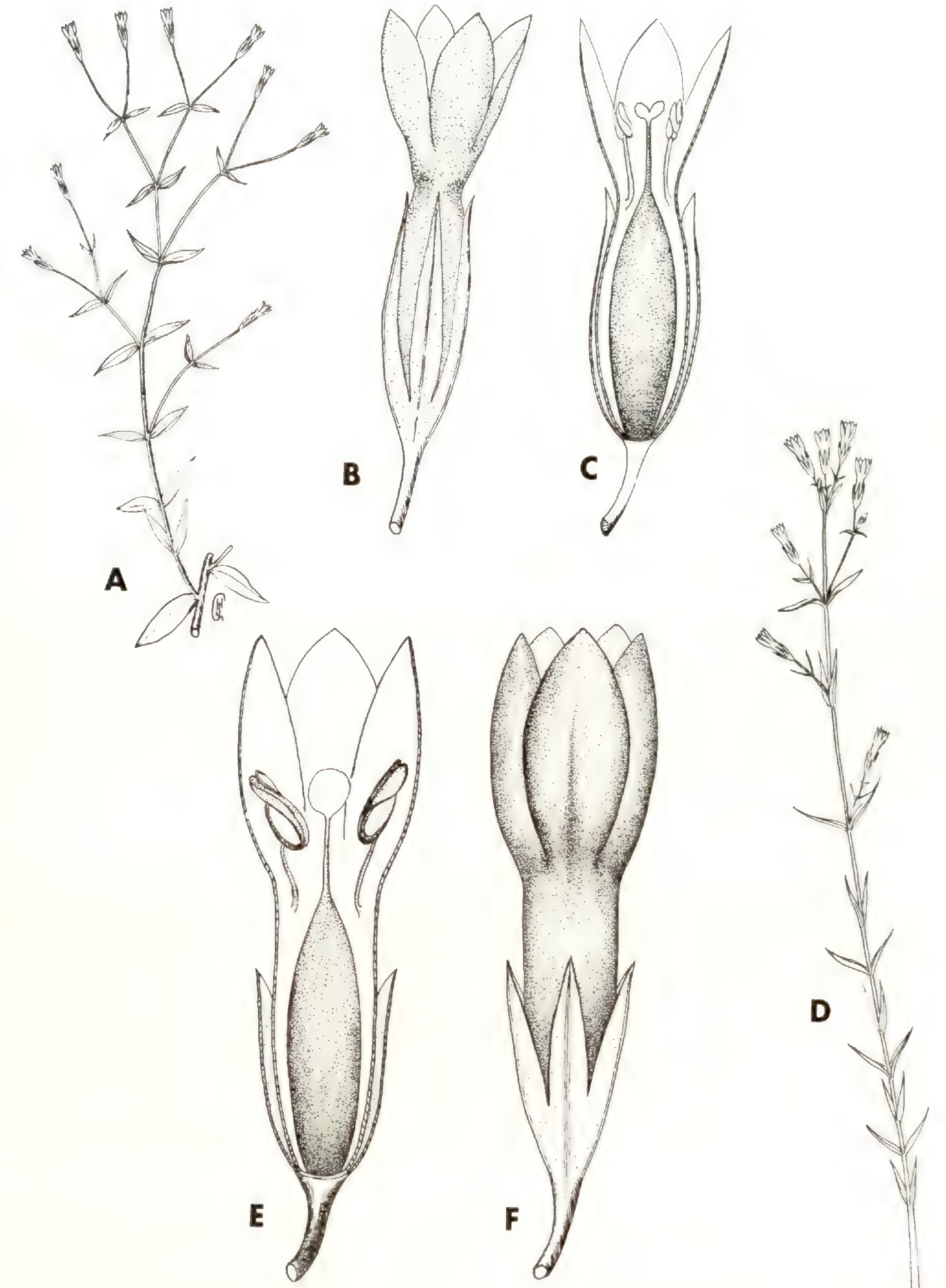


FIGURE 6. *Centaurium*.—A–C *C. quitense* (H.B.K.) Robinson.—A. Habit (× ½).—B. Flower (× 5).—C. Longitudinal section of flower (× 5).—D–F *C. strictum* (Schiede) Druce.—D. Habit (× ½).—E. Longitudinal section of flower (× 5).—F. Flower (× 5). [A–C after *White & White 104* (MO). D–F after *Terry 1358* (MO).]

inserted on the corolla tube ca. ½ from the base of the corolla, the filaments filiform, the anthers bilobate at the base, 1.5–2 mm long; pistil 0.6–1.2 cm long, the ovary fusiform, glabrous, the style ca. 2 mm long, the stigma included, shallowly bilobate. *Capsules* fusiform, 5–8 mm long, usually beaked by the persistent style; seeds suborbicular to pyriform to irregular, slightly flattened, the testa conspicuously loose-reticulate.

This pink-flowering herb occurs at high altitudes in Mexico and southward to the Province of Chiriquí in Panama.

CHIRIQUÍ: Volcán de Chiriquí, Potrero, 2300–3450 m on open hillside, *Davidson 893* (F, MO), *1014* (F). S slope of Volcán de Chiriquí, 3000 m, *Terry 1358* (F, MO).

2. **Centaurium quitense** (H.B.K.) Robinson, Proc. Amer. Acad. Arts 45: 397. 1910.—FIG. 6A–C.

Erythraea quitensis H.B.K., Nov. Gen. Sp. Pl. 3: 178. 1819.

Herb, 7–30 cm tall, erect, densely divaricate-branched; stems 4-angular, narrowly winged. *Leaves* cauline, lanceolate, narrowly ovate to elliptic, acute to obtuse at the apex, slightly attenuate at the base, 0.6–1.8 cm long and 1–7 mm broad, thin-chartaceous, with (1–)3(–5) veins basally connate and inconspicuous. *Inflorescences* axillary and terminal, solitary on simple or reduced dichasia, several-flowered; the peduncles 4-angular, narrowly winged, 0.9–4.3 cm long; the pedicels 0.8–2.1 cm long. *Flowers* usually 4-merous, pink, 6–9 mm long; calyx 5–6 mm long, the lobes narrowly ovate, 4–5 mm long; corolla 6–9 mm long, infundibular, the lobes ovate, acute to obtuse at the apex, 2–4 mm long; stamens 3–3.5 mm long, inserted near the middle of the corolla tube and alternate with the lobes, slightly exserted, the filaments filiform, 2–2.5 mm long, the anthers ca. 1 mm long, bilobate at the base; pistil 4–5 mm long, the ovary ellipsoid, 2–3 mm long, the style ca. 2 mm long, the stigma distinctly bilamellate, the lobes capitate. *Capsules* fusiform, 6–8 mm long, ± beaked (persistent style); seeds orbicular, flattened, the testa conspicuously loose-reticulate.

Known from Guatemala to Peru.

CANAL ZONE: Between Fort Clayton and Corozal, along the old Las Cruces Trail, *Standley 29192, 29225* (both US). CHIRIQUÍ: Near Boquete, 1100–1400 m, *Lewis et al. 378* (MO); *Davidson 655* (F). S of El Boquete, Río Caldera, 1250 m, *Killip 3626* (US). Valley of the upper Río Chiriquí Viejo, *White & White 104* (MO). LOS SANTOS: 5–9 mi. from Chitre on road to Las Tablas, roadside, *Burch et al. 1223* (MO, NY).

This species occurs in high altitudes, however, two collections (*Standley 29192, 29225*) have been made near sea level in the Canal Zone. The two lowland collections are considerably taller than those from Chiriquí.

7. SCHULTESIA

Schultesia Mart., Nov. Gen. Sp. Pl. 2: 103. 1826.

Herbs, erect, annuals, branched or unbranched; stems terete to angulate, occasionally with an inconspicuous wing. *Leaves* cauline, sessile, usually ovate to obovate, sometimes narrowly so, obtuse, acute to short-acuminate apically, usually amplexicaul at the base, chartaceous to submembranous. *Inflorescences*

terminal or axillary, few- to many-flowered or 1-flowered by reduction of a simple dichasium, simple or compound dichasia, bracteate. *Flowers* often large and showy, usually white, pink or lavender; calyx 4-parted, tubular, cupular or urceolate, 4-carinate to 4-winged, the lobes longer or shorter than the tube; corolla infundibular, ± constricted above the ovary, 4-lobed, the lobes usually ovate to triangular, contorted in aestivation; stamens usually 4, included to slightly exserted, the filaments filiform, basally dilated to form a membranous wing, the anthers oblong, erect, usually with an inconspicuous apical mucro; pistil included, ovary 1-locular, the placenta slightly to considerably intruded, the style filiform, deciduous, the stigma bilobate. *Capsules* septicidally 2-valvate, surrounded by the marcescent calyx and corolla; seeds small, numerous, foveolate. *Pollen grains* united in a usually tetrahedral tetrad, 44–77 μ; single grains 3-colporate (3-colpate, 3-porate), the concurrent colpi of two contiguous grains ca. 15 × 13 μ, the ora usually not confluent, the colpus margin and adjacent areas of exine often patternless, the colpus membrane granulose, the diameter of apocolpia 18–25 μ; exine 2–6 μ thick at the distal poles, decreasing in thickness towards equator; sexine thicker than nexine, reticulate, heterobrochate, the lumina 0.5–7 μ or 0.5–2 μ in diameter, the muri 0.5–1 μ wide; nexine smooth or granulose (*S. guianensis*, *S. heterophylla*, *S. lisianthoides*).

The pollen of the genus *Schultesia* is similar to that of *Coutoubea*; *S. guianensis* has markedly stout and thick bacules; *S. heterophylla* has commonly rhomboidal tetrads; *S. lisianthoides* consistently differs from the other species, having on the average smaller tetrads and a finer reticulate pattern.

A neotropical genus of annual herbs containing 20 to 25 species with 4 known from Panama.

a. Calyx 1.2–4.6 cm long, conspicuously winged, the wing (1.5–)2–3 mm broad.
  b. Flowers 4–5.7 cm long; the calyx wing inconspicuously veined; the corolla lobes 1.3–2.1 cm long ..... 1. *S. heterophylla*
  bb. Flowers 1.6–2.6 cm long; the calyx wing with conspicuous dense-reticulate veins; the corolla lobes 0.6–0.8 cm long ..... 2. *S. guianensis*
aa. Calyx 0.6–0.9 cm long, carinate, unwinged or very narrowly winged, the wing when present less than 1 mm broad.
  c. Inflorescences of few- to many-flowered simple or compound dichasia; leaves more crowded toward the base ..... 3. *S. lisianthoides*
  cc. Inflorescences 1-flowered by reduction of simple dichasia; leaves uniformly distributed along the stem ..... 4. *S. pohliana*

1. **Schultesia heterophylla** Miq., Linnaea 19: 137. 1847.

S. hayesii Robinson, Proc. Amer. Acad. Arts 45: 399. 1919.

Herb, 9–70 cm tall; stems erect, sparingly branched, the branches strongly ascending, subterete basally, becoming quadrangular above, slightly winged. *Leaves* usually shorter than the internodes, the lamina of the basal leaves narrow-elliptic to ovate, acute to subacuminate at the apex, amplexicaul at the base, the upper leaves linear-triangular to narrowly ovate, long acuminate at the apex, amplexicaul at the base, the leaves 2–8 cm long and 1.5–6.5 mm broad, 1–3-nerved, the main veins basally connate, chartaceous to submembranous. *Inflorescences* in the upper axils and terminal, borne singly or in simple, few-

flowered dichasia; the pedicels 0–2 mm long (flowers usually sessile); the bracts foliose. *Flowers* 4–5.7 cm long, rose-pink to bright pink; calyx 3.2–4.6 cm long, urceolate, winged, the wing 2–3 mm broad, inconspicuously veined, the lobes linear-triangular, long-acuminate, slightly flaring; corolla 4–5.7 cm long, the throat constricted above the ovary, the lobes broadly obovate, obtuse and minutely mucronate at the apex, flaring, 1.3–2.1 cm long; stamens 2.6–4 cm long, included, inserted on the corolla tube ca. ⅓ from the base, the filaments flattened near the point of insertion to form a winged, apically bidentate appendage, the anthers 4–5 mm long, slightly twisted, bilobate at the base; pistil 1.7–3 cm long, the ovary 8–15 mm long, ca. 2.4 mm in diameter, the style 9–15 mm long, the stigma lobes flattened, oblong, to 2–3 mm long. *Capsule* fusiform, subdiscoid, 12–18 cm long, surrounded by the persistent calyx and marcescent corolla; seeds ca. 0.2–0.4 mm long, compressed, inconspicuously reticulate.

West Indies, Central and South America.

This species has often been confused with *Schultesia brachyptera*. They are, however, easily separated; *S. heterophylla* having distinctly membranous wings on the calyx lobes, while the calyx lobes of *S. brachyptera* are merely ridged and lack membranous wings.

CANAL ZONE: Along the old Las Cruces Trail, between Fort Clayton and Corozal, *Standley 29196* (US). Río Grande Station, Panama Railway, *Hayes 160* (GH, holotype *S. hayesii*). COCLÉ: Aguadulce in savannas, *Pittier 2322* (US). Near Casa Larga, wet savanna, *Allen 2969* (GH, MO). Near Chepo, sabanas, *Hunter & Allen 20* (MO). Chico, marshy land, *Killip 3237* (US). Agricultural experiment station at Matías Hernández, *Pittier 6870* (MO). Near Matías Hernández, *Standley 28867* (MO). Between Matías Hernández and Juan Díaz, *Standley 31985* (US). 1 mi. E of Juan Díaz, *Killip 3263* (US). In marsh near Juan Díaz, *Standley 26223* (US). Along road between Panamá and Chepo, *Dodge et al. 16629* (MO). Near Las Sabanas, *Standley 40785* (US). Nuevo San Francisco, wet savanna, *Standley 30742* (US). Near Pacora, *Allen 986* (GH, MO). E of Río Tocumen, near the big swamp, *Standley 26711* (US). VERAGUAS: Hills W of Sona, *Allen 1069* (F).

2. **Schultesia guianensis** (Aubl.) Malme, Arkiv. Bot. 3(12): 9. 1904.

Exacum guianensis Aubl., Hist. Pl. Guiane Fr. 68, *pl. 26, fig. 1.* 1775.
Schultesia stenophylla Mart., Nov. Gen. Sp. Pl. 2: 106, *pl. 182.* 1827.

Herb, 5–35 cm tall; stems erect, unbranched or sparsely branched, the branches strongly ascending, 4-angular, slightly winged. *Leaves* uniformly distributed along the stem; the lamina of the basal leaves ovate, the upper ones narrowly ovate to linear, 0.8–4.7 cm long and 2–8 mm broad, acute to subobtuse at the apex, attenuate to amplexicaul at the base, the lateral veins 1–3, the veins basally connate, inconspicuous, thin-chartaceous. *Inflorescences* in the upper axils and terminal, borne singly or in simple or compound, few-flowered dichasia; the pedicels to 4 mm long (flowers usually sessile to subsessile); the bracts foliose, narrowly ovate to linear, to 22 mm long and to 4 mm broad. *Flowers* 1.6–2.6 cm long, dull pale to dirty pink; calyx 1.2–2.2 cm long, urceolate, winged, the wing (1.5–)2–3 mm broad, the densely reticulate veins conspicuous, the lobes narrowly ovate, long-attenuate at the apex, 6–10 mm long; corolla 1.6–2.6 cm long, infundibular, the throat constricted below, the lobes obovate to subspathulate, rounded to subacute at the apex, 6–8 mm long, covered with numerous, minute, dark purple spots; stamens included, 13.5–16 mm long, inserted basally

on the corolla tube, the filaments 12–14 mm long, the anthers 1.5–2 mm long, bilobate at the base with an inconspicuous mucro; pistil exserted, the ovary fusiform, 8–10 mm long, the style 7–9 mm long, the stigma lobes discoid, ca. 2 mm in diameter. *Capsule* fusiform, 12–14 mm long; seeds irregular, ca. 0.5 mm long.

Mexico southward in Central America to Panama.

CANAL ZONE: Between Fort Clayton and Corozal, along the old Las Cruces Trail, *Standley 29193* (US). COCLÉ: Near Natá, *Allen 831* (MO). PANAMÁ: Near Casa Larga, *Allen 2970* (MO). Pacora, roadside, *Killip 3083* (US). Near Punta Paitilla, moist thicket, *Standley 26238, 26296* (both US). Near Juan Franco Race Track, Panamá, *Standley 27807* (US). Sabana de Juan Corso, near Chepo, *Pittier 4677* (US). Between Pacora and Chepo, boggy grasslands and marginal thickets, *Woodson et al. 1647* (MO). Las Sabanas, *Standley 25910* (US); *Bro. Heriberto 154* (US); *Bro. Paul 342* (US). San José Island, *Johnston 192* (GH).

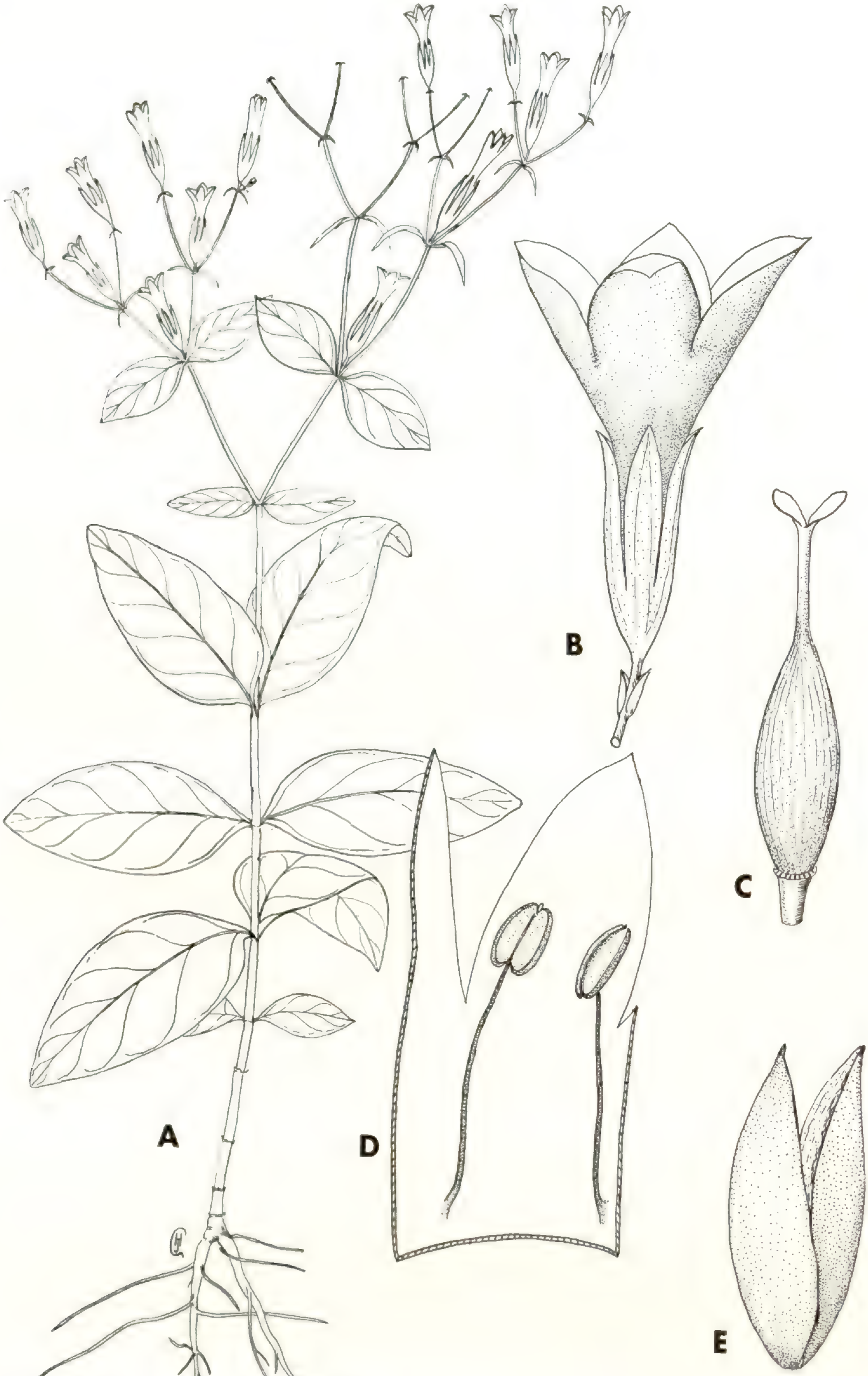
3. **Schultesia lisianthoides** (Griseb.) Benth. & Hook. *ex* Hemsley, Biol. Centr. Amer. 2: 348. 1882.—FIG. 7.

Xestea lisianthoides Griseb., Linnaea 22: 35. 1849.

Herb, 7–90 cm tall; stems terete, erect, unbranched or sparsely branched, the branches strongly ascending. *Leaves* more crowded toward the base; the lamina ovate, ovate-elliptic, elliptic, oblong to obovate, 1.5–10 cm long and 0.5–4.5 cm broad, acute to short-acuminate at the apex, attenuate to amplexicaul at the base, the lateral veins pinnate, 4–6 pairs, inconspicuous, thin-chartaceous. *Inflorescences* axillary and terminal, borne in simple or compound dichasia, few- to many-flowered; the pedicels 1–10 mm long; the bracts narrowly ovate, to 20 mm long and 5 mm broad. *Flowers* 1–1.7 cm long, pink to lavender; calyx 6–7 mm long, cupular, the lobes fused only at the base, carinate, the margins membranous; corolla 1–1.7 cm long, the lobes triangular, acute at the apex, 2–4 mm long and 2–3 mm broad; stamens 4–5 mm long, inserted on the corolla tube ca. ½ way from the base of the corolla, the filaments 3–3.5 mm long, the anthers ca. 1.5 mm long with an inconspicuous mucro; ovary 4–5 mm long, ca. 2.5 mm in diameter, fusiform, the style 2–3 mm long, the stigma lobes oblong, ca. 1 mm long and 0.5 mm broad. *Capsule* fusiform, 6–9 mm long, 2–3 mm in diameter; seeds irregular, ca. 0.5 mm long.

Southern Mexico, Central America and northern South America.

CANAL ZONE: Balboa, grassy slopes, *Standley 30898* (US); *Foster s.n.* (US). Barro Colorado Island, *Shattuck 845* (F, MO); *Robyns 65-21* (MO). Near Corozal, *Piper 5303* (F, US). Cerro de Ancón, *Celestine 80* (US). Along Río Chagres between Gamboa and Alajuela, *Allen 671* (F, US). Between Fort Clayton and Corozal, along the old Las Cruces Trail, wet field, *Standley 29220* (US). Las Cascades Plantation near Summit, *Standley 29638* (US). Darién Station, open bank, *Standley 31650* (US). Río Grande near Culebra, *Pittier 2090* (US). In government forest along Las Cruces Trail, *Hunter & Allen 671* (MO). Hills between Río Grande and Pedro Vidal on road to Arraiján, *Pittier 2707* (US). Near Miraflores Lake, *White 274* (MO). Near Miraflores Locks, *Greenman & Greenman 5203* (MO). Río Pedro Miguel, near East Paraíso, *Standley 29970* (US). Summit, weedy field, *Standley 26963* (US). CHIRIQUÍ: Near San Félix, *Pittier 5233* (MO). COCLÉ: Penonomé and vicinity, *Williams 234* (US). COLÓN: Between France Field and Cativa1, moist thicket, *Standley 30379* (US). 9 mi. S of Puerto Armuelles, *Liesner 161* (MO). HERRERA: Near Ocú, *Stern et al. 1704* (MO). 4 mi. S of Los Pozos, *Tyson 2645, 2657* (both MO). LOS SANTOS: 3 mi. S of Carreta, ca. 5 mi. S of Las Tablas, *Burch et al. 1227* (MO). 11 mi. N of Tonosí, *Tyson et al. 2957* (MO).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PANAMÁ: Cerro Azul, *Dwyer 1978* (MO). Sabanas near Chepo, *Hunter & Allen 61a* (MO). Savannas, *Macbride 2647* (F, US). Near Juan Franco Race Track, Panamá, in savanna, *Standley 27727* (US). Near Matías Hernández, moist thicket, *Standley 28967* (US). Tumba Muerto Road, *Standley 29708* (US). Near Punta Paitilla, moist thicket, *Standley 26237* (US). Between Las Sabanas and Matías Hernández, *Standley 31833* (US). San José Island, *Johnston 1095* (GH, MO, US).

4. **Schultesia pohliana** Prog. *in* Mart., Fl. Bras. 6(1): 205, *tab. 56, fig. 1.* 1865.

Herb to ca. 35 cm tall; stems slender, terete to subangulate, smooth to slightly winged, unbranched or sparingly 2- to 3-branched above, the branches strongly ascending, the internodes exceeding the leaves. *Leaves* uniformly distributed along the stems, linear, 1–1.8 cm long and 2–3 mm broad, obtuse to acute at the apex, becoming amplexicaul at the base, the lateral veins inconspicuous, submembranous. *Inflorescences* terminal, 1-flowered by reduction of simple dichasia; the pedicel 6–12 mm long. *Flowers* 1.4–1.8 cm long, rose; calyx tube 8–9 mm long, narrowly urceolate, the lobes 5–6 mm long, triangular, carinate, ± erect, the margins membranous; corolla 1.4–1.8 cm long, the lobes 4–6 mm long, stamens subequal, 4–5 mm long, inserted midway on the corolla tube, the filaments winged toward the base, the anthers linear, 1.5–2 mm long, minutely mucronate; ovary 2–3 mm long, the style 6–8 mm long, the stigma lobes oblong, ca. 1 mm long. *Capsule* unknown.

A poorly known species of South America that apparently ranges into Central America only in Panama.

COCLÉ: Aguadulce, in savannas, *Pittier 4946* (US).

8. SYMBOLANTHUS

Symbolanthus G. Don, Gen. Syst. 4: 210. 1837.

Herbs, shrubs or rarely small trees; stems usually branched, erect, tetragonal, often slightly winged on the angles. *Leaves* short petiolate; the petioles amplexicaul; the lamina generally ovate, elliptic to oblong, subrotund to acuminate at apex, narrow tapering at base, membranous to coriaceous, the costa prominent, the lateral veins becoming obscure. *Inflorescences* of few-flowered cymes or the flowers solitary, terminal or infrequently axillary. *Flowers* bracteate, 5-merous, long-pedicellate; calyx campanulate, the lobes free to near the base, carinate; corolla usually pink, sometimes purple, often broadly salverform, the lobes erect to spreading at anthesis, ovate; stamens equalling or exceeding the corolla tube, the filaments inserted on the lower half of the corolla tube, expanded basally, the anthers sagittate; ovary ovate, 1-locular, the paired placentae parietal along the 2 sutures, the style filiform, the stigma bilamellate, the lobes linear to oblong, flattened. *Capsules* generally surrounded by the marcescent calyx and corolla, ovate to ellipsoid, septicidally 2-valvate; seeds small, cubical, appearing tuberculate. *Pollen grains* united in tetrahedral tetrads,

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FIGURE 7. *Schultesia lisianthoides* (Griseb.) Benth. & Hook. *ex* Hemsley.—A. Habit (× 1).—B. Flower (× 4).—C. Gynoecium (× 5).—D. Interior portion of corolla showing two stamens (× 6).—E. Fruit (× 6). [After *Stern et al. 1704* (MO).]

65–98 μ; single grains 3-colporate (3-colpate, 3-porate), the concurrent colpi of 2 contiguous grains ca. 15 × 6 μ, the diameter of apocolpia 25–30 μ; exine 4–6 μ thick at the distal poles, 7–8 μ thick at equator; sexine thicker than nexine, reticulate, heterobrochate, differentiated into a coarsely reticulate, ± equatorial zone with lumina 2–20 μ in diameter, the muri 1–5 μ wide, usually supported by one row of bacules, and for the rest a more delicate reticulum with lumina 0.5–5 μ in diameter, the muri 1–2 μ wide; nexine smooth or granulose (*S. pulcherrimus*).

This genus contains approximately 15 poorly known species in Bolivia, Peru and Colombia and extends into Panama and Costa Rica. Only one species is known with certainty from Panama.

1. **Symbolanthus pulcherrimus** Gilg, Bot. Jahrb. (Syst.) 22: 344. 1896.—FIG. 8.

Tall woody *herb* or shrub, 1.5–4 m high, the branchlets tetragonous, occasionally winged, becoming subterete. *Leaves* with petioles to 1.5(–3) cm long; lamina elliptic to narrowly elliptic, long-attenuate into the petiole, acuminate at the apex, to 14.5(–22) cm long and 7(–9) cm wide, thin-chartaceous, the costa prominent and the lateral veins subprominulous beneath. *Inflorescences* of 5–7-flowered cymes at the apex of branches and branchlets or the flowers borne solitary. *Flowers* with the pedicels to 2.5 cm long, the bracts triangular, to 5 mm long; calyx to 2.6 cm long, the lobes united basally for ca. 0.7–0.8 mm, ovate, obtuse to acute apically, obtusely carinate dorsally, to 1 cm wide, coriaceous to membranous along the margins; corolla deep pink, to 10 cm long, the tube cylindric-infundibuliform, to 1.8 cm in diameter at the throat, the lobes apparently erect, broadly ovate, acute-acuminate, 2–2.2 cm long; stamens equalling the corolla tube, the filaments inserted ca. 1–1.5 cm above the base of the corolla tube, filiform, enlarged-triangular at the base with 5 short, triangular, membranous scales opposite the filaments, (fide Gilg, not noticed in Panamanian material), the anthers to 5 mm long, 2-lobed at the base, mucronate at the apex; style slightly exserted, the stigma conspicuously and broadly 2-lobed, the lobes to 6 mm long. *Capsule* broadly ellipsoid, 3–3.8 cm long and 1.8–2.5 cm broad, conspicuously beaked by the persistent basal portion of the style; seeds cubical, ca. 1 mm square.

Costa Rica and Panama.

Another collection, *Kirkbride & Duke 1330* (MO) from the Province of Darién, is tentatively placed with *Symbolanthus pulcherrimus*. This collection differs by having a more slender corolla tube and the corolla lilac rather than pink. Although this may represent a second taxon of the genus in Panama, the paucity of collections from Panama prevents any accurate assessment of variation.

BOCAS DEL TORO: Robalo Trail, Northern slopes of Cerro Horqueta, 6000–7000 ft, frequent, *Allen 4946* (BR, MO). CHIRIQUÍ: Humid forest between Alto de las Palmas and top of Cerro de la Horqueta, 2100–2268 m, *Pittier 3223* (US). DARIÉN: Cerro Pirre, *Bristan 518* (MO). Summit of Cerro Pirre, *Gentry & Clewell 6988, 6989* (both MO).

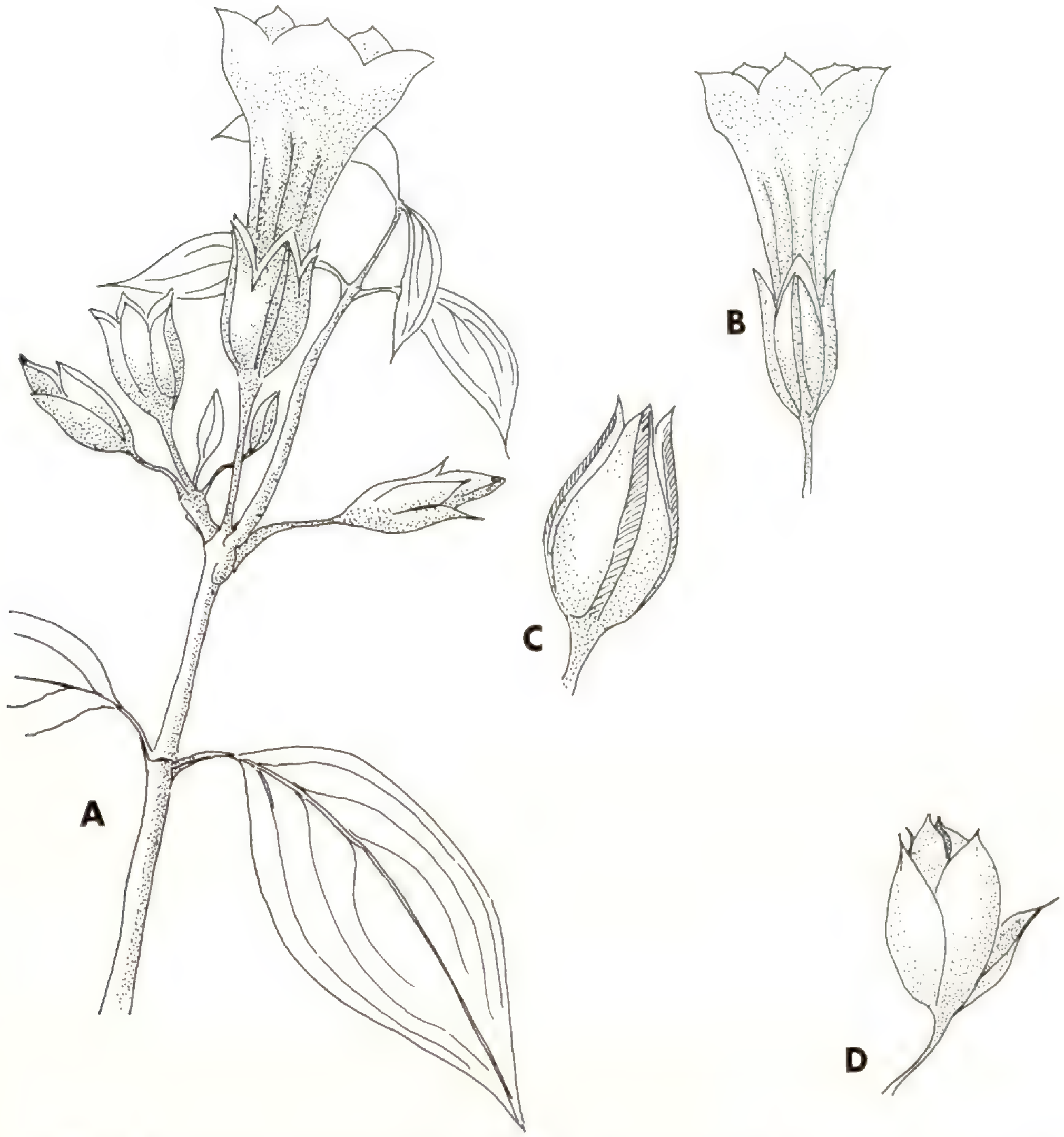


FIGURE 8. *Symbolanthus pulcherrimus* Gilg.—A. Habit (× ½).—B. Flower (× ½).—C. Flower bud showing carinate calyx lobes (× 1½).—D. Fruit showing marcescent calyx (× 1).

9. CHELONANTHUS

Chelonanthus Gilg *in* Engl. & Prantl, Nat. Pfl. 4(2): Abt. 2: 98. 1895.

Herbs, mostly annuals, rarely suffrutescent; the stems usually simple, erect, tetragonal and often slightly winged. *Leaves* sessile to short-petiolate, amplexicaul; the lamina generally ovate, acute to acuminate at the base, membranous to subcoriaceous, the costa prominent. *Inflorescences* of terminal or axillary, simple or compound dichasia, pedunculate. *Flowers* 5-merous, white, greenish, yellow, rose or bluish, slightly zygomorphic, bracteate; calyx cupuliform to campanulate, the lobes imbricate, carinate; corolla infundibular, the tube gibbous, the lobes erect to slightly flaring; stamens 5, included to shortly ex-

serted, the filaments adnate to the lower half of the corolla tube, the anthers usually reflexed, sagittate at base; ovary 2-locular (1-locular with much intruding placentae), sessile, the style filiform, persistent, the stigma bilobate. *Capsules* surrounded by the marcescent calyx and corolla, generally ovoid, septicidally 2-valvate; seeds tiny, variously angulate, the testa often reticulate. *Pollen grains* united in tetrahedral tetrads, 52–77 μ; single grains 3-colporate (3-colpate, 3-porate), the concurrent colpi of two contiguous grains ca. 15 × 5 μ, the diameter of apocolpia 25–30 μ; exine 2–4 μ thick at the distal poles, 6–10 μ at equator; sexine thicker than nexine, reticulate, heterobrochate, differentiated into a coarsely reticulate, ± equatorial zone with lumina 0.5–9 μ in diameter, the muri 1–5 μ wide, unevenly thickened, occasionally fragmented into ± rounded processes, and for the rest a more delicate reticulum with lumina 0.5–2 μ in diameter, the muri 0.5–1.5 μ wide, occasionally not connected laterally, of a pilum or clava-like shape; nexine smooth or granular (*C. alatus*).

1. **Chelonanthus alatus** (Aubl.) Pulle, Enum. Vasc. Pl. Surinam 376. 1906.—FIG. 9.

Lisianthus alatus Aubl., Hist. Pl. Guiane Fr. 204, *pl. 80.* 1775.

Herb, 1–5 m tall; stems erect, tetragonal to subterete, slightly winged on the angles, green. *Leaves* with the lamina broadly ovate to ovate-elliptic, attenuate at the base, acute to short acuminate at the apex, 4–18 cm long and 2.7–10.3 cm wide, thin-chartaceous, the lateral veins in 2 pairs, strongly arcuate, the costa and veins conspicuous beneath. *Inflorescences* axillary or terminal, borne in large laxly-flowered simple or compound dichasia, often appearing racemose; the peduncles 3.5–14 cm long, terete to subangulate; the pedicels 4–11 mm long, the bracts narrowly ovate, 2–3 mm long. *Flowers* 2.2–3.2 cm long; calyx 4–6 mm long, cupular, the lobes 2–3 mm long, ovate to subrotund, the margins ± membranous; corolla 2.2–3.2 cm long, greenish-yellow, the lobes 5–7 mm long and 6–8 mm wide at the base, ovate, acute at the apex, erect; stamens included or short-exserted, the filaments inserted ca. ¼ from the base of the corolla, filiform, 1.4–2 cm long, the anthers reflexed, inconspicuously mucronate apically; pistil 2–3 cm long, included or short exserted, the ovary oblongoid, 4–6 mm long, 3–4 mm in diameter, the style terete, thickened, the stigma of 2 flattened oblong lobes, the lobes 3–4 mm long, 6–8 mm in diameter, beaked, the beak (persistent style) to 1.8 cm long; seeds tetragonal to slightly irregular, the testa reticulate, 0.2–0.3 mm long.

Mexico, Central America and southward to Brazil.

A common large herb known locally in Panama as "arbol de mal casada" (*Aviles 50*).

CANAL ZONE: Between Summit and Gamboa, *Greenman & Greenman 5236* (MO). Pipeline road, *Croat 12744* (MO). Pipeline Road within 5 mi. of Gamboa Gate, *D'Arcy & D'Arcy 6198* (C, MO). Paraíso, *Dwyer 7160* (MO). Road C-21, *Duke 5768* (GH, MO). 1 mi. N of Summit, *Tyson et al. 2764* (GH, MO); *Tyson & Blum 1950* (MO). C-2 of Fort Clayton, *Harvey 5111* (F). Las Cascadas plantation near Summit, *Standley 29572* (US). Río East Paraíso, *Standley 29835* (US). Río Pedro Miguel near East Paraíso, *Standley 30022* (US). Obiso, *Standley 31738* (US). Barro Colorado Island, *Aviles 50* (F); *Croat 4368* (MO); *Shattuck 473* (F, MO); *Woodworth & Vestal 710* (F, GH, MO). Frijoles, *Ebinger 635* (MO).

FIGURE 9. *Chelonanthus alatus* (Aubl.) Pulle.—A. Node showing leaf (× ½).—B. Inflorescences showing flowers and fruits (× ¾).—C. Flower (× 1½).—D. Longitudinal section of flower (× 1½).—E. Gynoecium (× 2½).—F. Fruit (× 2).

Road C-21, 3 mi. from Gaillard Highway, *Croat 13004* (MO). COCLÉ: Hills S of El Valle de Antón, *Allen 2800* (MO, US). COLÓN: Between Río Piedras and Puerto Pilón, *Lewis et al. 3228* (COL, MO, UC). Portobelo, *D'Arcy & D'Arcy 6681* (MO). About 1 mi. W of Portobelo, *Gentry 1740* (MO). 4 mi. SW of Portobelo, *Croat 14110* (MO). Santa Rita, *Correa & Dressler 1036* (A, MO). Santa Rita Ridge, *Croat 15301* (MO). Lumber road about 8 km NE of Santa Rita, *Wilbur & Weaver 10869* (MO). Wooded slopes on Santa Rita Ridge about 5 mi. from highway at Sabanita, *Wilbur & Luteyn 11843* (MO). Near Sabanita, *Croat 11073* (MO). CHIRIQUÍ: Near San Félix, *Pittier 5431* (US). Finca Lerida to Boquete, *Woodson et al. 1111* (GH, MO). Ca. 1 mi. SW of Boquete, *Allen 4723* (MO). DARIÉN: Cana and vicinity, *Williams 822* (US). PANAMÁ: Cerro Campana, *Allen 2093* (F, GH, MO, US); *Duke 8670* (MO); *Correa & Dressler 371* (A, MO); *Lewis et al. 1911* (GH, MO, US), *3050* (COL, MO, UC); *Weaver & Foster 1696* (DUKE); *Kirkbride 256* (MO); *Tyson 6442* (MO).

10. MACROCARPAEA

Macrocarpaea (Griseb.) Gilg *in* Engl. & Prantl, Nat. Pfl. 4(2): 94. 1895.

Lisianthus sect. *Macrocarpaea* Griseb., Gen. Sp. Gent. 173. 1839.

Shrubs, subshrubs, rarely herbaceous, rarely epiphytic; branches rounded to quadrangular, longitudinally canaliculate, the internodes short to elongated. *Leaves* cauline, subsessile to petiolate; the petiole often amplexicaul; the lamina obovate, ovate to lanceolate, acute to cuspidate at the apex, usually cuneate at the base, membranous to coriaceous. *Inflorescences* terminal and axillary, open cymose, paniculate, or rarely racemose, often few-flowered. *Flowers* 5-merous; calyx campanulate to subtubular, the lobes imbricate or rarely valvate, usually unequal; corolla white, yellow, greenish, or red, salverform, narrow to broadly campanulate, rarely tubular, the lobes usually unequal, usually ovate; stamens adnate at or near the middle of the corolla tube, generally included, the filaments flattened, the anthers versatile, usually ovate, bilobate at the base; pistil often exserted, the ovary fusiform to pyriform, the style filiform, elongate, the stigma bilobate, often deeply so. *Capsules* ovoid to fusiform, often beaked by the persistent style, septicidally 2-valvate; seeds numerous, minute. *Pollen grains* in monads, radially symmetrical, isopolar, oblate, spheroidal, the amb rounded-triangular, 41–45 × 46–53 μ, 3-colporate to 3-porate, the colpi relatively short with rounded ends, the colpus membrane granulose, the ora lalongate to lolongate, the pores oval to circular, the diameter of apocolpia (apoporia) 35–36 μ; exine 3–4 μ thick; sexine thicker than nexine, reticulate, heterobrochate, the lumina 0.5–10 μ in diameter, usually rounded, the muri 1–3 μ wide, supported by one or usually more rows of bacules, of a pilum- or clava-like shape with rounded to truncate apices; nexine generally granulose (*M. browallioides*).

Principally a shrubby genus of northern South America, especially of the Andes, but extending into the Greater Antilles and into Central America. Three species are known from Costa Rica and a fourth occurs in the mountainous region of western Panama.

Literature:

Ewan, J. A revision of *Macrocarpaea*, a neotropical genus of shrubby Gentians. Contr. U. S. Natl. Herb. 29: 209–249. 1948.

Weaver, R. E., Jr. The genus *Macrocarpaea* (Gentianaceae) in Costa Rica. Jour. Arnold Arbor. 53: 553–557. 1972.

1. **Macrocarpaea browallioides** (Ewan) A. Robyns & S. Nilsson, Bull. Jard. Bot. Natl. Belgique 40: 13, *figs. 1–15.* 1970.

Lisianthius browallioides Ewan, Proc. Biol. Soc. Washington 64: 132. 1951. (As "*Lisianthus*".)

Shrub to 1.8 m high, epiphytic, branched, the branchlets subquadrangular, canaliculate. *Leaves* petiolate; the petioles slender, to 2 cm long; the lamina elliptic to ovate-elliptic, basally attenuate, apically acuminate to 8 cm long and 4.2 cm wide, chartaceous, dark green, densely and minutely black-tuberculate above, paler beneath. *Inflorescences* cymose, few-flowered. *Flowers* with the calyx campanulate, to 1.8 cm long, the tube short, ± 5-angular, slightly unequal, the lobes ovate-triangular, to 1.4 cm, chartaceous, acute to cuspidate at the apex, the margins scarious; corolla white, infundibuliform, 3.3–4.0 cm long, deeply lobate, the lobes ± unequal, ovate-triangular, acute to acuminate at the apex, to 1.5 cm long, the margins inconspicuously erosulose; stamens ± exserted, the filaments inserted ca. 6–7 mm above the base of the corolla tube, the anthers 5–6 mm long, obtuse at the apex, deeply bilobate at the base, longitudinally dehiscent; ovary pyriform, the style filiform, the lobes of the stigma ± flattened, erect, to 2.5 mm long, papillate on the inner surface. *Capsule* unknown.

A poorly known species whose epiphytic habit is in need of verification.

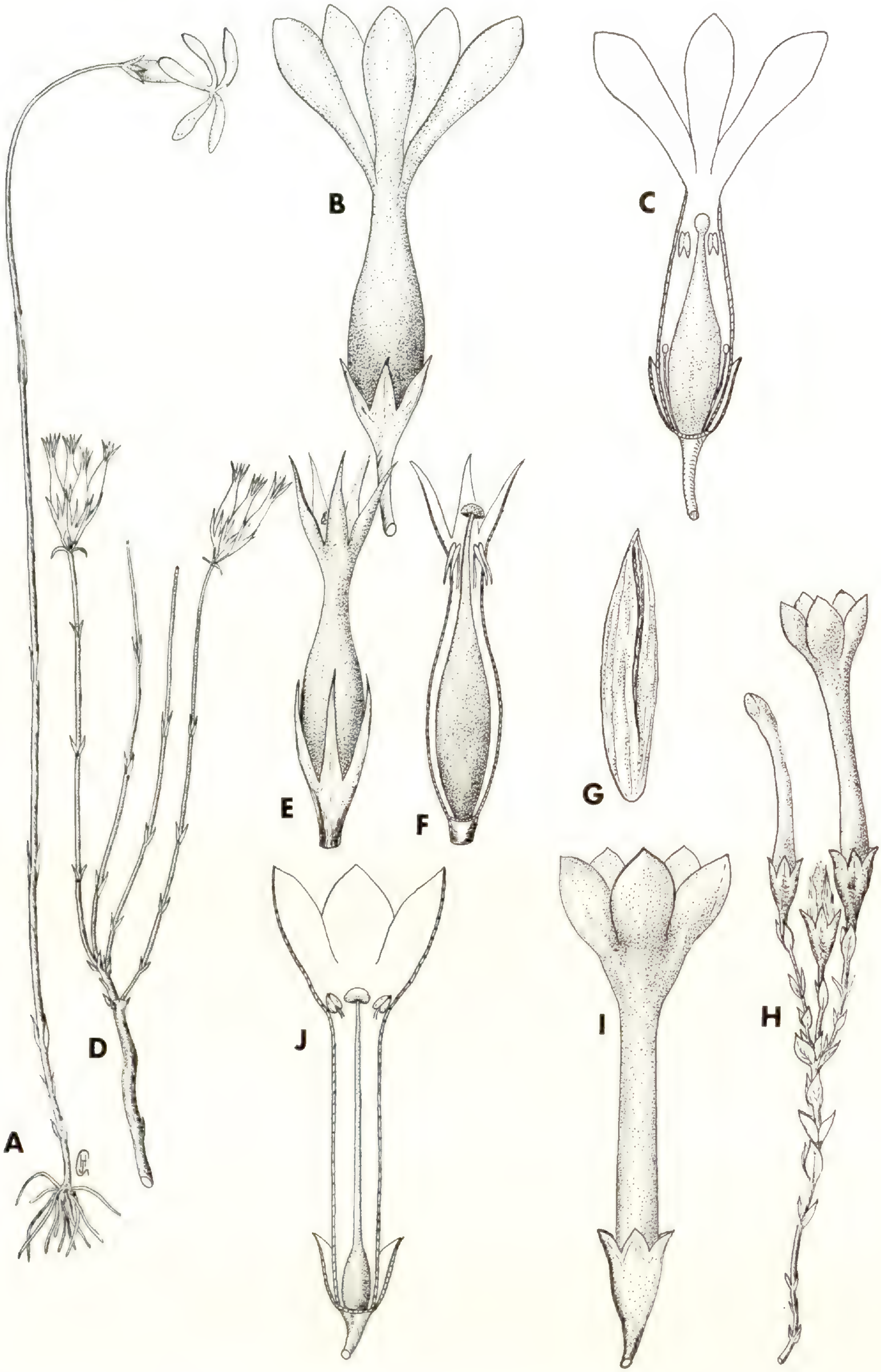
BOCAS DEL TORO: Northern slopes of Cerro Horqueta, Robalo Trail, 2000–2330 m, *Allen 4932* (MO).

11. LAGENANTHUS

Lagenanthus Gilg *in* Engl. & Prantl, Nat. Pfl. 4(2): 99. 1895.

Shrubs or sometimes climbing herbs or epiphytic and becoming woody, branching near the base; branches terete to ± angulate, slender, jointed, usually nodose. *Leaves* short-petiolate; the lamina subcoriaceous to ± succulent, ovate to lanceolate, short- to long-acuminate at the apex, often becoming caudate apically, rounded to attenuate at the base, the costa and lateral veins prominent or not beneath. *Flowers* 5-merous, terminal, solitary or in few-flowered corymbs, short-pedicellate; calyx broadly campanulate or narrowly tubular, the lobes ovate or subulate; corolla showy, salmon-pink throughout, or red basally and yellow apically, the tube abruptly or gradually inflated, abruptly constricted at the throat, the lobes obsolete to small or linear-oblong, usually reflexed; stamens included to shortly exserted, the filaments inserted near the base of the corolla tube, the anthers linear to oblong, basifixed, rounded to ± emarginate at the apex; the style cylindrical, included to exserted, the stigma bilobate. *Capsules* splitting septicidally, beaked by the persistent style; seeds irregularly covered with numerous short projections, dark brown on drying. *Pollen grains* united in tetrahedral tetrads, 62–66 μ; single grains 3-porate, the pores well-defined and circular, 6–8 μ in diameter, the pores of 2 contiguous grains separated by the reinforced, internal walls; exine 4 μ thick; sexine thicker than nexine, reticulate, heterobrochate, the lumina 0.5–8 μ, the muri 1–1.5 μ wide (*L. princeps* from Colombia).

Lagenanthus contains only 2 species, the endemic Panamanian *L. parviflorus* and *L. princeps* (Lindl.) Gilg, a large showy-flowered species from Colombia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and Venezuela. Rarely collected and thus poorly known, the taxonomic position and affinities of this genus remain in question.

Literature:

Ewan, J. A review of the neotropical lisianthoid genus *Lagenanthus* (Gentianaceae). Mutisia 4: 1–5. 1952.

1. **Lagenanthus parviflorus** Ewan, Mutisia 4: 5. 1952.

Herb 1 m high, epiphytic (?); stems terete, nodose, ± succulent, fine-granulose, the epidermis irregularly ridged (when dried). *Leaves* with the petioles 3–5 mm long, terete, becoming indurate; the lamina narrowly ovate to ovate-elliptic, 4.8–15.5 cm long and 1.3–2.2 cm broad, long-acuminate at the apex, attenuate at the base, subcoriaceous, the costa with 4–6 inconspicuous, strongly ascending veins. *Inflorescence* unknown. *Flowers* terminal (cf. Ewan, 1952); calyx narrowly tubular, 13–14 mm long, the lobes filiform-subulate; corolla constricted at the base, abruptly expanded and inflated for most of its length, ± constricted at the apex, uniformly salmon-pink, 5–5.5 cm long, the lobes linear-oblong, 6–8 mm long and 1.5–2 mm broad, truncate at the apex, reflexed; stamens short-exserted, the filaments filiform, 4–4.5 cm long, the anthers oblong, 4–5 mm long; immature ovary slender (fide Ewan). *Capsule* unknown.

Known only from the somewhat fragmentary type, this species was collected in the floristically rich mountainous area in the Province of Coclé. The species has apparently not been collected since 1946.

COCLÉ: Region N of El Valle de Antón, 1000 m, *Allen 3601* (MO, holotype).

12. VOYRIA

Voyria Aubl., Hist. Pl. Guiane Fr. 208. 1775.

Biglandularia Karsten, Linnaea 28: 416. 1856.
Leiphaimos Auct. *non* Schlecht. & Cham., Linnaea 6: 387. 1831.

Herbs, saprophytic, devoid of chlorophyll, perennial; the stems usually erect, simple to sometimes branched. *Leaves* small, scale-like, opposite, decussate, sessile, the opposite pairs usually ± connate at the base. *Inflorescences* terminal and dichasial, or flowers mostly terminal and solitary. *Flowers* 4–6-merous; calyx tubular to campanulate, sometimes hyaline, occasionally provided within and at the base with a verticil of small scales, persistent; corolla variously colored, much longer than the calyx, marcescent, the tube elongated, the lobes contorted, spreading; stamens included, the filaments long or the anthers sessile, inserted below the throat of the corolla tube or on the corolla tube at various

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FIGURE 10. *Voyria*.—A–C. *V. tenella* Hook.—A. Habit (× 1).—B. Flower (× 3).—C. Longitudinal section of flower (× 3).—D–G. *V. alba* Standl.—D. Habit (× 1).—E. Flower (× 4).—F. Longitudinal section of flower (× 4).—G. Fruit (× 4).—H–J. *V. truncata* (Standl.) Standl. & Steyerm.—H. Habit (× 1).—I. Flower (× 1½).—J. Longitudinal section of flower (× 1½). [A–C after *Lewis et al. 2182* (MO). D–G after *Dodge & Hunter 8625* (MO) and *Dodge et al. 16927* (MO). H–J after *Allen 3783* (MO).]

heights, the anthers introrse, coherent or not, the thecae appendaged or not at the base; ovary sessile or shortly stipitate, eglandular or with 2 opposite glands at the base, the latter sometimes stipitate, 1-locular, the 2 parietal placentae sometimes protruding, style filiform, stigma usually simple, capitate or infundibuliform, rarely 2-lobed. *Capsules* surrounded by the persistent calyx and marcescent corolla, ellipsoid to oblong to linear, septicidally 2-valvate or only medially septicidal, the valves remaining united at the base and apex; seeds numerous, minute, ovoid and wingless or narrowly fusiform, *i.e.* provided with 2 long hair-like wings. *Pollen grains* in monads, bilateral, heteropolar, reniform, semi-ovidal to unsymmetrically biconvex, or radially symmetrical, isopolar, oblate to spheroidal, or irregular in shape, the outline in lateral view convexo-concave to convexo-plane to depressed ovate, or ± circular to irregular, in polar view circular to oval, or irregular, 7–12 × 11–21 × 9–14 μ, or 10–11 × 12–15 μ, or 14–15 μ in diameter, 1–2 porate (one pore often smaller), the pores 1–3 μ in diameter, the pore margin reinforced by a thickening (annulus) 0.5–1 μ wide, 1–2 μ high, consisting of sexine and/or nexine, the annulus occasionally absent; exine 0.5–1 μ thick, at the apertures up to 2 μ thick, the stratification obscure, non-baculate; sexine smooth or scabrous.

A tropical genus of about 16 species, mainly in Central and South America and the West Indies, with 1 species in tropical Africa; 9 species reported from Panama. Growing upon decayed leaves on forest floors.

Literature:

Raynal, A. Étude critique des genres *Voyria* et *Leiphaimos* (Gentianaceae) et révision des *Voyria* d'Afrique. Adansonia, sér. 2. 7: 53–71. 1967.

Robyns, A. Notes on some American species of *Voyria* (Gentianaceae). Ann. Missouri Bot. Gard. 55: 398–399. 1969.

Standley, P. C. The Panamanian species of *Leiphaimos*. *In* "Studies of tropical American phanerogams—No. 3." Contr. U. S. Natl. Herb. 20: 194–200. 1919.

Williams, L. O. *Voyria* and *Leiphaimos*. *In* "Tropical American plants, IX." Fieldiana: Bot. 31: 411–415. 1968.

a. Inflorescences dichasial.
  b. Herb entirely white; flowers sessile or subsessile; opposite scales connate at the base only; corolla 10–11 mm long, the tube constricted ca. 2 mm below the apex, glabrous within ---------- 1. *V. alba*
  bb. Herb with orange to purplish-yellow stems; pedicels 2–8 mm long; opposite cauline scales connate for ca. ⅙–½ of their length; corolla orange or yellow, 15–20 mm long, the tube cylindric, scarcely dilated at the throat, villosulous towards the apex within ---------- 2. *V. aurantiaca*

aa. Flowers solitary.
  c. Calyx without scales at the base within; ovary eglandular.
    d. Anthers sessile or filaments short, not exceeding 1 mm.
      e. Anthers exappendiculate.
        f. Opposite cauline scales connate for ca. ⅕–⅓ of their length or less; cauline scales narrowly ovate, acute apically; calyx lobes narrowly ovate-triangular, acute to acuminate apically; corolla lobes acuminate apically; anthers sessile; ovary substipitate, narrowly ellipsoid ---------- 3. *V. aphylla*
        ff. Opposite cauline scales connate for ca. ½–⅔ of their length; cauline scales broadly to very broadly ovate, obtuse to rounded apically; calyx lobes broadly ovate, obtuse apically; corolla lobes obtuse apically; anthers

with filaments 0.5–1 mm long; ovary sessile, oblong, apically truncate ..... 4. *V. truncata*

ee. Anthers prolonged basally into hairy appendages ca. 1.5 mm long ..... 5. *V. stellata*

dd. Anthers with the filaments 5–15 mm long.

g. Corolla to 2.5 cm long; filaments 5–7 mm long, inserted ca. ½ or ca. ⅔ above the base of the corolla tube ..... 6. *V. pittieri*

gg. Corolla to 3.5 cm long; filaments ca. 15 mm long, inserted ca. 1 cm above the base of the corolla tube ..... 7. *V. pulcherrima*

cc. Calyx provided within and at the base with a verticil of emarginate scales; ovary with 2 opposite glands.

h. Corolla pale blue; ovary very shortly stipitate, with 2 appressed stipitate glands at the base, the basal part of the stipe adnate to the ovary, the upper part ca. 1–2 mm long and free; stigma capitate ..... 8. *V. tenella*

hh. Corolla orange; ovary sessile, with 2 narrowly elliptic glands ca. 0.5 mm above the base; stigma 2-lobed ..... 9. *V. bilobata*

1. **Voyria alba** (Standl.) L. O. Wms., Fieldiana: Bot. 31: 413. 1968.—Fig. 10D–G.

Leiphaimos albus Standl., Contr. U. S. Natl. Herb. 20: 198. 1919.

Herb, 5–20 cm high, entirely white; the stem erect, sometimes decumbent at the base, usually simple (to the inflorescence) or sometimes with 1–3 erect branches from the base, glabrous throughout. *Scales* membranous, the opposite scales connate at the base, triangular, long-acuminate at the apex, 2–4 mm long, much shorter than the internodes. *Inflorescences* dichasial, the dichasia simple or compound and few-flowered. *Flowers* 5-merous, sessile or subsessile, each subtended by 2 opposite bracts similar to the cauline scales but smaller; calyx tubular, ca. 3–4 mm long, the lobes narrowly triangular, cuspidate at the apex, ca. 1.5 mm long, the sinuses obtuse; corolla 10–11 mm long, the tube constricted ca. 2 mm below the apex, glabrous inside, the lobes narrowly triangular, acuminate at the apex, ca. 2.5 mm long and 0.7 mm wide at the base; stamens inserted somewhat below the throat of the corolla tube, the filaments very short and ca. 0.5 mm long, the anthers coherent, oblong, ca. 0.6 mm long, each theca prolonged basally into a subulate appendage about as long as the anther; gynoecium ca. 8.5 mm long, the ovary sessile, narrowly oblong, eglandular, ca. 5.5 mm long and 1.2–1.3 mm in diameter, the style ca. 3 mm long, the stigma capitate and minutely tuberculate. *Capsule* medially septicidal; seeds wingless.

Panama and Colombia.

CANAL ZONE: Barro Colorado Island, *Brown 152a* (F); *Croat 6663, 11180* (both MO); *Dodge s.n.* (MO); *Graham 325* (GH); *Hayden 132* (MO); *Hunnewell 16458* (GH); *Kenoyer 495* (US); *Wheeler s.n.* (MO). COLÓN: Along trail to triangulation station on top of Tumba Vieja, 90–200 m, *Dodge et al. 16927* (MO, US). Loma de la Gloria, near Fató (Nombre de Dios), forests, 10–104 m, *Pittier 4094* (US). PANAMÁ: Hills between Capira and Potrero, 8–130 m, *Dodge & Hunter 8625* (MO). Hills NE of Hacienda La Joya, 50–300 m, forest floor on decaying leaves, *Dodge et al. 16874* (MO). SAN BLAS: Forest around Puerto Obaldía, 0–50 m, *Pittier 4295* (US, holotype; GH, isotype).

2. **Voyria aurantiaca** Splitg., Tijdschr. Natuurl. Gesch. Physiol. (Leiden) 7: 135. 1840.

Leiphaimos aurantiaca (Splitg.) Miq., Stirp. Surin. Select. 149. 1850.
L. thalesioides Standl., Contr. U. S. Natl. Herb. 20: 198. 1919.

L. stenoloba Johnston, Sargentia 8: 243. 1949.
Voyria thalesioides (Standl.) L. O. Wms., Fieldiana: Bot. 31: 414. 1968.

Herb to 18 cm high; the stems orange to purplish-yellow, 1 to several, fastigiately branched at the base, erect, simple or few-branched, slender, terete, glabrous. *Scales* membranous, ± hyaline, the opposite cauline scales connate for ca. ⅙–½ their length, the cauline scales narrowly ovate, acuminate-subulate at the apex, to 6 mm long and ca. 2 mm wide, much shorter than the internodes, the basal scales much shorter. *Inflorescences* dichasial, loose, to 7-flowered. *Flowers* 5-merous, the pedicels 2–8 mm long; calyx colorless, campanulate, 5–6 mm long, the lobes narrowly triangular, long-acuminate-subulate at the apex, about as long as the tube, the sinuses rotund; corolla orange or yellow, 15–20 mm long, the tube cylindric, scarcely dilated at the throat, 12–16 mm long, ca. 1–1.5 mm in diameter, villosulous towards the apex but below the insertion of the stamens within, the lobes spreading, narrowly ovate, acute to abruptly acute apically, 3–4 mm long; stamens inserted somewhat below the throat of the corolla tube, the filaments short, to 1 mm long, the anthers scarcely coherent, oblong, ca. 1 mm long, the thecae shortly apiculate-appendaged at the base, the appendages ca. 0.5 mm long; gynoecium 10–14 mm long, eglandular, the style slender, 5–7 mm long, the stigma capitate, minutely tuberculate, ca. 1 mm in diameter. *Capsule* narrowly oblong, acute apically, to 8 mm long, completely dehiscent; seeds wingless.

British Honduras, Panama and Surinam.

PANAMÁ: San José Island, Loop road near start of Little Butch Trail, in moist leaf mold on densely forested slope in deep shade, *Johnston 380* (GH); hill N of Cross Roads, in deep leaf mold on sheltered moist shaded slope, *Johnston 1116* (GH, holotype of *L. stenoloba*). SAN BLAS: Hills of Sperdi, near Puerto Obaldía, 20–200 m, *Pittier 4351* in part (US, type of *L. thalesioides*).

3. **Voyria aphylla** (Jacq.) Pers., Syn. Pl. 1: 284. 1807. (As "*Vohiria*".)

Gentiana aphylla Jacq., Select. Stirp. Amer. Hist. 87, *pl. 60, Fig. 3*. 1763.
Voyria uniflora Lam., Tabl. Encycl. Méth. Bot. 1: 491. 1797.
Exacum aphyllum (Jacq.) Willd. *in* L., Sp. Pl., ed. 4 (*i.e.* 5). 638. 1797.
Leiphaimos aphylla (Jacq.) Gilg *in* Engl. & Prantl, Nat. Pfl., ed. 1. 4(2): 104. 1895.
L. costaricensis Standl., Contr. U. S. Natl. Herb. 17: 433. 1914.
L. lutea Morton, Jour. Washington Acad. Sci. 27: 310. 1937.

Herb to 20(–25) cm high; the stem white or yellowish, erect, simple, slender, terete, glabrous. *Scales* membranous, the opposite cauline scales connate for ca. ⅕–⅓ their length or less at the base, the cauline scales few, distant, narrowly ovate, acute apically, 5–8 mm long, much shorter than the internodes, glabrous. *Flowers* solitary, 5-merous, rather large to 6 cm long, the pedicels short or sometimes elongated (when short, the calyx is said to be subtended by a pair of bracteoles, *i.e.* the upper pair of cauline scales); calyx hyaline, cylindric-campanulate, to 7.5 mm long, the lobes narrowly ovate-triangular, acute to acuminate apically, ca. ⅓ as long as the tube, the sinuses acute; corolla yellow, to 6 cm long, the tube narrowly cylindrical, longitudinally slightly ribbed, somewhat constricted above the ovary and below the anthers, to 48 mm long, the lobes spreading, ovate or narrowly ovate, acuminate at the apex, to 12 mm long, inconspicu-

ously puberulous toward the base within; anthers sessile, inserted somewhat below the throat of the corolla tube, free (or sometimes coherent?), broadly oblong, ca. 1–1.25 mm long, exappendiculate; gynoecium to 4.2 cm long, the ovary substipitate, narrowly ellipsoid, to 20 mm long, eglandular, the style filiform, to 22 mm long, the stigma capitate, ca. 1.5 mm in diameter. *Capsule* medially septicidal; seeds winged, filiform-fusiform, to 1 cm long.

Costa Rica, Panama, northern South America and the West Indies.

BOCAS DEL TORO: Near Chiriquí Lagoon in swampy land, *Wedel 1153* (MO). COCLÉ: Cerro Pajita, region N of El Valle de Antón, 1100 m, *Allen 3794* (MO). DARIÉN: Cerro de Garagará, Sambú basin, 500–974 m, *Pittier 5654* (US).

4. **Voyria truncata** (Standl.) Standl. & Steyerm., Field Mus. Nat. Hist., Bot. Ser. 23: 78. 1944.—FIG. 10H–J.

Leiphaimos truncatus Standl., Contr. U. S. Natl. Herb. 20: 196. 1919.
Voyria allenii Steyerm., Ann. Missouri Bot. Gard. 28: 460. 1941.

Herb to 18 cm high; the stem erect, stout, simple to few-branched, glabrous. *Scales* dull red, thin-cartilaginous (when dry), the opposite scales connate for ½–⅔ their length at the base, the cauline scales broadly to very broadly ovate, obtuse to rounded apically, 3–5 mm long, minutely ciliolate along the margins, the upper cauline scales somewhat shorter to somewhat longer than the internodes, the lower scales much shorter than the internodes. *Flowers* solitary, 5-merous, the pedicels thick, 4–9 mm long; calyx campanulate, 4.5–6 mm long, the lobes broadly ovate, obtuse apically, 1–3 mm long, minutely ciliolate along the margins; corolla pale yellow, cream-colored, bright pink, or purplish-lavender, to 5.5 cm long, the tube cylindric, scarcely dilated at the throat, 3–4 cm long, inconspicuously puberulous without towards the apex, the lobes spreading, ovate, obtuse apically, 7–15 mm long, inconspicuously ciliolate along the margins, inconspicuously puberulous within especially towards the base; stamens inserted in the upper half of the corolla tube, ca. 3–7 mm below the throat, the filaments short, 0.5–1 mm long, the anthers coherent, broadly oblong to subglobose, exappendiculate, to 1.3 mm long; gynoecium to 3.6 cm long, the ovary sessile, oblong, truncate apically, to 8–9 mm long, glabrous, eglandular, the style filiform, to 2.7 mm long, the stigma capitate-peltate, the margins sinuate. *Capsule* to 1.5 cm long and 5 mm in diameter; seeds wingless.

Guatemala, Nicaragua and Panama; very close to the Colombian *V. macrantha* Killip.

BOCAS DEL TORO: Old Bank Island, Chiriquí Lagoon, *Wedel 2159* (MO). CANAL ZONE: Barro Colorado Island, Wheeler Trail, 960 m marker, *Croat 4296a* (MO). Forest along road to Battery VII, *Johnston 1728* (A). COCLÉ: Hills N of El Valle de Antón, dense shade, 800 m, *Allen 2240* (F, holotype of *V. allenii*). Cerro Pajita, hills N of El Valle, terrestrial, 1100 m, *Allen 3783* (MO). N rim of El Valle de Antón, near Cerro Turega, terrestrial, 650–700 m, *Woodson & Schery 190* (MO). PANAMÁ: Cerro Campana, 1000 m, *Allen 2416* (GH). SAN BLAS: High hills back of Puerto Obaldía, 50–200 m, *Pittier 4306a* (US, holotype).

5. **Voyria stellata** (Standl.) A. Robyns, Ann. Missouri Bot. Gard. 55: 400. 1969.

Leiphaimos stellatus Standl., Contr. U. S. Natl. Herb. 20: 197. 1919.

Herb, 4–18 cm high; the stem erect, very slender, simple, terete, glabrous to inconspicuously puberulous-papillate, especially toward the apex. *Scales* membranous, the opposite cauline scales connate for ¼–⅓ their length, the cauline scales narrowly ovate, long-acuminate-subulate at the apex, 3.5–9 mm long, much shorter than the internodes, the basal scales ovate and much shorter than the cauline scales. *Flowers* solitary, 5-merous, long-pedicellate, the pedicels slender, to 23 mm long; calyx pinkish or nearly colorless (fide Standley; somewhat orange when dry), oblong-cylindric and ± 5-angulate, 5–12 mm long, the lobes narrowly triangular, long-acuminate-subulate apically, carinate dorsally, 2.5–5 mm long, the sinuses acute; corolla orange-yellow to yellow, 1.5–3.1 cm long, inconspicuously puberulous outside, the tube cylindric, slightly dilated at the throat, 10–17 mm long, the lobes spreading, narrowly triangular to narrowly oblong-ovate, acuminate apically, 5–14 mm long and 1–3 mm wide; anthers subsessile, inserted ca. 1 mm below the throat of the corolla tube, coherent, oblong, ca. 1–1.2 mm long, the thecae rounded apically, prolonged basally into a hairy appendage ca. 1.5 mm long; gynoecium to 16 mm long, the ovary sessile, oblong-fusiform, gradually tapering into the style, eglandular, 4–7.5 mm long, the style slender, to 8 mm long, the stigma capitate, minutely tuberculate, ca. 1.5 mm in diameter. *Capsule* oblong-fusiform; seeds wingless.

Panama, Venezuela, Brazil and Peru.

DARIÉN: Cuna Reservation, Río Morti, 6 mi. upstream from Morti Arriba, 45–80 m, *Duke 8451* (MO). SAN BLAS: Mainland opposite Achituppu, from beach to 1.5 mi. inland, marshy rain forest, often by native plantations, *Lewis et al.* 98 (MO). Forests around Puerto Obaldía, 0–50 m, *Pittier 4294* (US, holotype).

6. **Voyria pittieri** (Standl.) L. O. Wms., Fieldiana: Bot. 31: 413. 1968.

Leiphaimos pittieri Standl., Contr. U. S. Natl. Herb. 20: 197. 1919.

Herb, 5–15 cm high; the stem erect, purplish, terete, usually simple, sometimes few-branched above, glabrous. *Scales* erect or appressed, membranous, purplish, the opposite scales connate at the base, narrowly ovate, long-acuminate to subulate at the apex, to 6–7 mm long, markedly shorter to subequalling the internodes. *Flowers* solitary, 5–6-merous, the pedicels 4–14 mm long; calyx purple, tubular-campanulate, 5–8 mm long, lobed to about the middle or slightly below, the lobes narrowly triangular, long-acuminate to subulate at the apex, 3–5 mm long, the sinuses acute; corolla lilac or pale blue, to 25 mm long, the tube narrowly cylindric in the lower ⅔, infundibuliform in the upper ⅓, slightly to conspicuously puberulous on the upper ½ inside, the lobes narrowly oblong to oblong, acuminate or cuspidate at the apex, sometimes abruptly so, 5–9.5 mm long, the sinuses obtuse to acute; stamens inserted ½ or ⅔ above the base on the corolla tube, the filaments slender-filiform, 5–7 mm long, slightly to densely puberulous, the anthers coherent, oblong, ca. 1 mm long, not appendaged; gynoecium ca. 14.5–15 mm long, the ovary sessile, oblong-fusiform, eglandular, ca. 2.5–3 mm long, the style slender, to 12 mm long, the stigma capitate and inconspicuously tuberculate. *Capsule* oblong-fusiform; seeds wingless.

Panama, Colombia and Venezuela.

COCLÉ: Mountains beyond La Pintada, 400–600 m, *Hunter & Allen 551* (MO). SAN BLAS: Forests around Puerto Obaldía, 40–50 m, *Pittier 4292* (US, holotype). Hills of Sperdi near Puerto Obaldía, 20–200 m, *Pittier 4351* in part (US).

7. **Voyria pulcherrima** (Standl.) L. O. Wms., Fieldiana: Bot. 31: 413. 1968.

Leiphaimos pulcherrimus Standl., Contr. U. S. Natl. Herb. 20: 199. 1919.

Herb to 15 cm high; the stem erect, simple below, sparsely fastigiate-branched above, the branches terete, purplish, the stem and branches inconspicuously puberulous especially toward the apex. *Scales* thick, the opposite scales connate for ca. ½ their length, rounded to obtuse apically, minutely ciliolate along the margins, to 5 mm long, much shorter than the internodes. *Flowers* solitary, 5-merous (sometimes 4-merous?), long-pedicellate, the pedicels slender, to 23 mm long; calyx purplish, oblong-campanulate, 5–6 mm long, the lobes broadly to very broadly ovate, ± rounded apically, minutely ciliolate along the margins, to 1.3 mm long; corolla bright yellow (fide Standley), to 35 mm long, the tube gradually dilated from the base to the throat, minutely papillose within, the lobes spreading, oblong-obovate, rounded at the apex, ca. 9 mm long and 6–7 mm wide; stamens inserted ca. 1 cm above the base on the corolla tube, the filaments slender-filiform, ca. 15 mm long, minutely pilose, the anthers coherent, narrowly oblong, ca. 2 mm long with short slender appendages at the base (fide Standley); gynoecium ca. 22 mm long, the ovary sessile, oblong, obtuse at the apex, eglandular, ca. 6 mm long, the style slender, ca. 16 mm long, the stigma capitate, short-conical, ca. 1.5 mm broad. *Capsule* unknown.

Known only from Panama.

SAN BLAS: High hills back of Puerto Obaldía, 50–200 m, *Pittier 4306* (US, holotype; GH, isotype).

8. **Voyria tenella** Hook., Bot. Misc. 1: 47, *pl. 25, fig. B.* 1829. (As "*Vohiria*".)—FIG. 10A–C.

Leiphaimos tenella (Hook.) Miq., Stirp. Surin. Select. 149. 1850.
Voyria simplex Griseb. *in* Seem., Bot. Voy. Herald 170. 1854.
Biglandularia azurea Karsten, Linnaea 28: 417. 1856.
Leiphaimos azurea (Karsten) Gilg *in* Engl. & Prantl, Nat. Pfl. 4(2): 105, *fig. 46*, L.M. 1895.
L. simplex (Griseb.) Standl., Contr. U. S. Natl. Herb. 20: 199. 1919.

Herb to 20 cm high; the stems simple, erect, colorless, slender, terete, glabrous; the roots short and tuberous. *Scales* few, membranous-hyaline, the opposite cauline scales connate for ca. ½ their length, the cauline scales distant, ovate, obtuse apically, to 5.5 mm long. *Flowers* solitary, 5-merous; calyx hyaline, campanulate, 2.5–4 mm long, the lobes ovate, obtuse apically, 1–1.8 mm long, the sinuses rather acute, provided within and at the base with a verticil of emarginate scales less than 0.5 mm long; corolla pale blue, to 23.5 mm long, the tube narrowly ovoid, not enlarged at the throat, 9–16 mm long, glabrous inside and out, the lobes spreading, narrowly oblong-obovate, obtuse at the apex, 4.5–7.5 mm long and 1.8–2.5 mm wide, deciduous; anthers sessile, inserted ca. 2–2.5 mm below the throat of the corolla tube, coherent, the thecae oblong, rounded-truncate apically, very shortly prolonged basally, ca. 1–1.2 mm long; gynoecium 7–13 mm long,

the ovary shortly stipitate, narrowly ellipsoid, 4–7 mm long, with 2 opposite, appressed, stipitate glands at the base, the basal part of the stipe adnate to the ovary, the upper part ca. 1–2 mm long and free, style 2–4 mm long, stigma capitate and to 1.5 mm in diameter. *Capsule* ellipsoid, medially septicidal; seeds winged, filiform-fusiform, to 1 cm long.

British Honduras (?), Costa Rica, Panama and northern South America.

BOCAS DEL TORO: Punta Peña, near Chiriquicito, rain forest, 330 m, *Lewis et al. 2182* (MO). CANAL ZONE: Barro Colorado Island, *Banham 470* (F); *Croat 4268, 4308, 6207* (all MO); *Hunnewell 16456* (GH); *Graham 324* (GH); *Sexton s.n.* (MO); *Shattuck 223, 1086* (both F); *Standley 40868* (US). Gatún, in forest, *Ostenfeld 87* (US). Hills N of Frijoles, wet forest, common in dark places, *Standley 27610* (US). Ft. Sherman, *Stevens 241* (US). New Limón, *Stevens 1024* (US). Ft. Sherman on Peña road, *Tyson & Chu 1697* (MO). COLÓN: Along trail to Triangulation Station on top of Tumba Vieja, in leaf mold, 90–200 m, *Dodge et al. 16926* (MO). Loma de la Gloria Fató (Nombre de Dios), 10–100 m, in forest, *Pittier 4081* (US). DARIÉN: Loma Cuasi, behind Manene, *Duke 13623* (MO). Puerto St. Dorotea, rich woods, *Dwyer 2284* (MO). Camp Summit, Darién-San Blas border along Sea Level Canal Route 17, seasonal evergreen forest and weedy clearing, *Oliver et al. 3696* (MO). PANAMÁ: Río La Maestra, *Allen 19* (MO). Hills between Capira and Potrero, woods, 140 m, *Dodge & Hunter 8624* (MO). Hills NE of Hacienda La Joya, on forest floor on decaying leaves, 50–300 m, *Dodge et al. 16873* (MO). San José Island, leaf mold in shaded damp forests, *Johnston 140* (GH). Abundant among dead leaves in darker parts of N forest, *Murphy s.n.* (GH). Chimán, rain forest, *Lewis et al. 3280* (MO). Cerro Azul, in deep shade, 650 m, *Tyson 2206* (MO). DARIÉN: Cuna Reservation, Río Mortí Arriba, terrestrial, 50–80 m, *Duke 8452* (MO). SAN BLAS: Forest around Puerto Obaldía, 0–50 m, *Pittier 4293* (GH, US).

9. **Voyria bilobata** A. Robyns, Ann. Missouri Bot. Gard. 55: 398, *fig. 1.* 1969.

Herb to 15 cm high; the stem erect, slender, terete, orange-red, simple or bifurcate, glabrous. *Scales* membranous, glabrous; scales on the upper part of the stem distant, to 5 mm long, much shorter than the internodes, ovate, acuminate apically, the opposite scales connate for ca. 2 mm at their base; scales on the lower part of the stem scarcely shorter, ± equalling the internodes. *Flowers* solitary, 5-merous, to 17 mm long; calyx tubular-campanulate, hyaline, obtusely 5-angulate, 5-lobate, ca. 4 mm long, provided within and at the base with 5 squamellae, the latter opposite the lobes, transversely elliptic, emarginate apically, ca. 0.5–0.6 mm wide, the lobes subequal, subacute at the apex, ca. 1 mm long and 0.8 mm wide at the base, the sinuses rounded; corolla orange, the tube narrowly cylindrical, somewhat ventricose around the ovary, scarcely dilated at the throat, ca. 10.5 mm long and ca. 2 mm in diameter, the lobes apparently spreading, narrowly oblong, acute apically, ca. 6–6.5 mm long and ca. 1.3 mm wide; anthers sessile, inserted below the throat of the corolla tube, coherent, 2-lobed at the base, ca. 1.5 mm long (appendices included), the thecae rounded at the apex, very short-appendiculate at the base, the appendices scarcely 0.5 mm long and inconpsicuously puberulous; gynoecium ca. 8–9 mm long, the ovary sessile, narrowly oblong, ca. 4.5–5 mm long, provided ca. 0.5 mm above the base with 2 opposite, narrowly elliptic glands ca. 1.5 mm long, style filiform and ca. 3.5–4 mm long, stigma 2-lobed, ca. 2 mm in diameter. *Capsule* unknown.

Known only from Panama.

BOCAS DEL TORO: Punta Peña, near Chiriquicito, 300 m, rain forest, *Lewis et al. 2181* (MO, holotype).

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FLORA OF PANAMA[1]

BY ROBERT E. WOODSON, JR. AND ROBERT W. SCHERY
AND COLLABORATORS

Part VIII

FAMILY 163. ASCLEPIADACEAE

DAVID L. SPELLMAN[2,3]

Mostly perennial *herbs, vines*, occasionally *shrubs* or small *trees*, some fleshy or cactus-like, generally with milky sap. *Leaves* opposite or whorled, simple, entire, sometimes caducous or vestigial, estipulate. *Inflorescence* generally cymose, the cymes usually umbelliform or racemiform, rarely paniculate. *Flowers* bisexual, actinomorphic, occasionally tending toward zygomorphy; calyx of 5 distinct or basally fused sepals which are imbricate or open in bud, generally with 1 or more glandular structures within the sinuses; corolla rotate, campanulate, urceolate, or funnelform, commonly white, pink, green, or brown-purple, shallowly or deeply 5-lobed, the lobes contorted or less commonly valvate in bud, the tube sometimes terminated by the faucal annulus, a low ridge or ring of tissue; stamens 5, inserted at or near the base of the corolla, the filaments flattened and short, usually connate to form a tube which is united to the stigma to form the gynostegium, a corona usually present, simple or of 5 or more lobes, adnate to the corolla throat or free from it but originating from the filaments, its structure highly variable, the anthers introrsely 2-celled, rarely 4-celled, sometimes with a sterile dorsal appendage of variable form, the connective often apically produced into a thin membranous appendage; pollen rarely in tetrads (Periplocoideae), mostly agglutinated into waxy masses (pollinia), these usually solitary in each anther cell and combined in pairs through a yoke mechanism consisting of a translator arm which connects each pollinium to a hardened black or brown ± trullate gland or corpusculum, the corpusculum situated between the anthers and adnate to the stigma disc; ovary of 2 distinct carpels, superior and included within the staminal tube, styles 2, short and distinct but united at the stigma, the stigma 1, peltately dilated into a usually pentagonal disc which is apically flattened, depressed, convex, umbonate, or rostrate, the ovules numerous in each carpel, pendulous and imbricate upon the lateral placentae. *Fruit* usually a single follicle resulting from the abortion of one carpel, generally ovoid to somewhat fusiform, the exocarp smooth or variously ornamented with tubercular or muricate projections, sometimes

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longitudinally winged, glabrous or pubescent, ventrally dehiscent; seeds compressed, usually with a marginate or emarginate wing, the seed coat thick or ± membranaceous, narrowed apically and usually bearing a tufted micropylar coma of long silky hairs; embryo large, the endosperm thin.

The Asclepiadaceae are a large family of wide distribution in tropical and temperate areas. The complex structure of the flower has been used to divide the family into a large number of small, mostly indistinct genera. Various authors have recognized in excess of 250 genera and more than 1800 species on a worldwide basis. Woodson (1941), in an attempt to render order to the chaotic array of genera, reduced the North American representatives of the family to nine genera.

In the New World, the Asclepiadaceae occupy nearly every type of habitat from Canada to southern Chile. The North American center of distribution of the family is southern Mexico and northern Guatemala, and the number of species becomes fewer as one goes south. Williams (1969) treated 90 taxa in the *Flora of Guatemala*, while in Panama, there are about half that number.

Of the 43 taxa recognized in the present treatment, 12 are found elsewhere in Central and South America, 3 are known only from Mexico and Central America, 9 are South American, 13 are endemic, and 2 are widespread throughout the tropics. Of the present endemic members, most are morphologically tied to the South American element of the family, and may eventually be recorded from there.

All 9 of the genera recognized by Woodson for North America occur in Panama.

Plants of this family are of little economic importance, except a few of horticultural use, most notably species of *Hoya*, *Stephanotis*, *Stapelia*, and *Cryptostegia*. Young fruits of some species are used as vegetables, either cooked or fresh, in Central and South America. Many members of the family are toxic to humans and livestock.

Because of the specialized characters involved in the identification of the Asclepiadaceae, three keys are included here. The first, based on natural characters following Woodson's (1941) concepts, is written to encompass the genera as they exist beyond the limits of Panama. An artificial key based solely on Panamanian material attempts to characterize the genera without reliance on more technical characters. The third key is based on fruiting characters of taxa occurring in Panama for which fruits are known.

Literature:

Williams, L. O. Flora of Guatemala. Fieldiana: Bot. 24, part VIII(4): 407–472. 1969.

Woodson, R. E., Jr. The North American Asclepiadaceae. I. Perspective of the genera. Ann. Missouri Bot. Gard. 28: 193–244. 1941.

KEY TO THE GENERA—Based on natural characters.

a. Pollen granular, united into tetrads, not agglutinated into sac-like pollinia; flowers 4 cm or more long, pink to purplish (Periplocoideae) ---------- 1. *Cryptostegia*

aa. Pollen agglutinated into sac-like pollinia; flowers 3 cm long or less, variously colored (Asclepiadoideae).
b. Pollinia pendulous, their faces uniformly flattened or rounded, uniformly fertile up to the point of attachment of the translators (Asclepiadeae).
c. Plants erect or nearly so, herbaceous, not scandent.
d. Corolla rotate, lobed nearly to the base, the lobes strongly reflexed at anthesis; corona of 5 cucullate hoods ---------- 2. *Asclepias*
dd. Corolla campanulate, lobed to about the middle, the lobes spreading; corona of 5 fleshy segments upturned at the base ---------- 3. *Calatropis*
cc. Plants scandent, herbaceous or somewhat woody.
e. Translators conspicuously thickened and appendaged near their attachment to the corpusculum; corolla lobes linear, 15–20 mm long; leaves ovate-cordate ---------- 4. *Oxypetalum*
ee. Translators not conspicuously thickened or appendaged; corolla not linear, less than 15 mm long; leaves various.
f. Corona of 5 separate, laminate scales, not inflated ---------- 5. *Cynanchum*
ff. Corona of 5 expanded bladder-like segments.
g. Corona of 5 small semi-vesicular sacs not basally connate, attached separately to the backs of the anthers; plants glabrous; leaf bases generally rounded ---------- 6. *Blepharodon*
gg. Corona of 5 closed vesicles basally connate by a fleshy ring and attached separately to the backs of the anthers; plants glabrous or pubescent; leaf bases acute to truncate or cordate ------- 7. *Sarcostemma*
bb. Pollinia horizontal or erect, their faces uniformly rounded and fertile to point of attachment of the translators or one or both faces indented, with a sterile hyaline margin near the point of attachment of the translators.
h. Pollinia strictly erect, their faces uniformly rounded, uniformly fertile to the attachment of the translators (Tylophoreae).
i. Corolla infundibular, urceolate, or campanulate, never strictly rotate nor waxy white in color.
j. Corolla less than 10 mm long, usually red, green, or yellow ---- 8. *Marsdenia*
jj. Corolla much greater than 20 mm long, white ---------- 9. *Stephanotis*
ii. Corolla rotate, flowers in pedunculate umbels, waxy white in color - 10. *Hoya*
hh. Pollinia horizontal or nearly so, occasionally ascending or descending, but one or both faces indented, and with a sterile hyaline margin near the point of attachment of the translators (Gonolobeae).
k. Corolla lobes conspicuously crispate; anthers conspicuously hypertrophied and vesicular throughout ---------- 11. *Fischeria*
kk. Corolla lobes not conspicuously crispate; anthers not conspicuously hypertrophied and vesicular.
l. Anthers without dorsal appendages; pubescence usually of long brown hairs overtopping shorter bulbous ones (glabrous in *M. mediocris*) ---
---------- 12. *Matelea*
ll. Anthers with spreading ± laminate, fleshy dorsal appendages; glabrous or pubescence not as above ---------- 13. *Gonolobus*

ARTIFICIAL KEY TO THE GENERA—Based on Panamanian material.

a. Plants erect, not at all scandent or procumbent.
b. Corolla campanulate, lobes purple tipped, not reflexed at maturity ... 3. *Calotropis*
bb. Corolla rotate, lobes red-orange or green, strongly reflexed at maturity . 2. *Asclepias*
aa. Plants scandent, climbing or procumbent.
c. Plants glabrous throughout or at least on the upper surface of the leaves.
d. Leaf bases shallowly or deeply cordate.
e. Inflorescences open, an elongate raceme or a large panicle of racemes ....
---------- 5. *Cynanchum*
ee. Inflorescences condensed, appearing umbellate, never paniculate.
f. Leaves heart-shaped; corolla lobes orange-brown, reflexed .... 12. *Matelea*
ff. Leaves not heart-shaped; corolla lobes brownish-red or green, not reflexed.
g. Flowers brownish-red, corolla tube evident ---------- 8. *Marsdenia*

gg. Flowers green, corolla rotate, the tube not evident without dissection.
h. Flowers less than 1 cm wide ..... 13. *Gonolobus*
hh. Flowers more than 2 cm wide ..... 12. *Matelea*

dd. Leaf bases various but not cordate.
i. Flowers large and showy, corolla tube more than 2 cm long; cultivated and escaping.
j. Flowers pink to purple ..... 1. *Cryptostegia*
jj. Flowers waxy white ..... 9. *Stephanotis*
ii. Flowers smaller, corolla tube less than 1 cm long; cultivated or native.
k. Flowers white (sometimes greenish tinged) or white with purplish blotches.
l. Flowers white with purple spots; corolla lobes linear .... 8. *Marsdenia*
ll. Flowers uniformly white; corolla lobes various but not linear.
m. Corolla 5 mm or less in diameter ..... 5. *Cynanchum*
mm. Corolla usually 10 mm or more in diameter.
n. Thick coarse vines with thick leaves, flowers waxy white; cultivated species ..... 10. *Hoya*
nn. Slender vines with thin leaves, flowers white but not waxy; native species.
o. Inflorescence umbellate, 20- or more flowered ..... 7. *Sarcostemma*
oo. Inflorescence a contracted raceme, usually less than 10-flowered ..... 6. *Blepharodon*

kk. Flowers variously colored, not white.
p. Flowers brownish-red, distinctly tubular, in dense umbelliform clusters ..... 8. *Marsdenia*
pp. Flowers green or yellowish, tube distinct or inconspicuous, in few flowered contracted racemes or 2- to several-flowered umbelliform clusters.
q. Flowers yellow to greenish yellow, with or without a distinct tube, in 2- to several-flowered umbelliform clusters .... 8. *Marsdenia*
qq. Flowers distinctly green, without a distinct tube, in few-flowered contracted racemes.
r. Flowers 2 cm or more in diameter, corolla lobes spreading ..... 13. *Gonolobus*
rr. Flowers less than 1 cm in diameter, corolla lobes reflexed ..... 12. *Matelea*

cc. Plants distinctly pubescent, at least on the upper surfaces of the leaves.
s. Plants with long, brown, spreading, multicellular hairs on stems and leaves, these usually dense on the younger stems.
t. Corolla lobes contorted-crispate on the margins ..... 11. *Fischeria*
tt. Corolla lobes never contorted-crispate at the margins ..... 12. *Matelea*
ss. Plants without long, brown, spreading, multicellular hairs, pubescence usually whitish or buff.
u. Leaf blades rounded at the base; flowers white ..... 7. *Sarcostemma*
uu. Leaf blades cordate at the base; flowers greenish-yellow, or green.
v. Corolla rotate, the tube not evident, less than 2 mm long .... 13. *Gonolobus*
vv. Corolla campanulate or with a distinct tube more than 5 mm long.
w. Corolla campanulate, the lobes linear and ribbon-like .... 4. *Oxypetalum*
ww. Corolla tubular or rotate ..... 8. *Marsdenia*

KEY TO SPECIES—Based mainly on fruiting material.

a. Plants erect, follicles smooth.
b. Fruits fusiform, attenuate apically, less than 2 cm in diameter .... *Asclepias curassavica*
bb. Fruits irregularly ovoid, not attenuate apically, more than 3 cm wide ..... *Calotropis procera*

aa. Plants scandent, follicles smooth or variously appendaged.
c. Follicles smooth, glabrous or pubescent, sometimes longitudinally striate, but not winged, ridged, or tuberculate.

d. Fruits finely puberulent overall, ± fusiform.
e. Leaves basally rounded; fruit 5–8 cm long, ca. 1.5 cm thick, apically acute ..... *Sarcostemma clausum*
ee. Leaves basally cordate; fruit size variable, apically long acuminate.
f. Fruit mostly less than 9 cm long, 2 cm thick ..... *Sarcostemma bilobum*
ff. Fruit mostly more than 9 cm long, 2–3 cm thick ..... *Oxypetalum cordifolium*
dd. Fruits glabrous or the pubescence minute and confined to the base and apex.
g. Fruits usually paired, abruptly narrowed toward the apex, 5 cm long or less.
h. Fruits ca. 5 cm long, 0.8 cm thick; inflorescences simple, umbellate ..... *Cynanchum infimicola*
hh. Fruits 3–4 cm long, ca. 0.5 cm thick; inflorescences compound, a panicle of umbels ..... *Cynanchum apocynellum*
gg. Fruits not paired, not abruptly narrowed toward the apex, more than 6 cm long.
i. Fruits fusiform; leaves basally rounded.
j. Fruits 15–20 cm long; stems with warty excrescences ..... *Marsdenia rotheana*
jj. Fruits less than 10 cm long; stems not warty.
k. Fruits 8–10 cm long, ca. 1 cm thick; stems and leaves glaucous ..... *Sarcostemma glaucum*
kk. Fruits 6–9 cm long, ca. 1.5 cm thick; stems and leaves not glaucous ..... *Blepharodon mucronatum*
ii. Fruits ellipsoid to ovoid; leaves basally rounded to cordate.
l. Follicles ovoid, longitudinally striate, 12–16 cm long, 4.5–5 cm thick; leaves basally rounded ..... *Marsdenia margaritaria*
ll. Follicles ellipsoid, not striate, 5–25 cm long, 2–10 cm thick; leaves basally cordate.
m. Inflorescence a simple raceme or large panicle of racemes; leaves thin-succulent; follicles variable in size.
n. Inflorescence racemose; follicles 5–10 cm long, 2–3 cm thick ..... *Cynanchum magdalenicum*
nn. Inflorescence a panicle of racemes; follicles 15–21 cm long, 7–10 cm thick ..... *Cynanchum cubense*
mm. Inflorescence a compact umbelliform cluster; leaves subcoriaceous; fruits 18–22 cm long, ca. 5 cm thick ..... *Marsdenia maculata*
cc. Follicles with longitudinal wings, thick ridges, or with tuberculate or digitiform projections.
o. Fruits glabrous, with 3–7 longitudinal wings, or a single cockscomb-like ridge at the base of the dorsal surface.
p. Fruits ellipsoid, woody, with a thick, low, single dorsal ridge ca. 3 cm long near the insertion of the pedicel, 21–30 cm long, 9–12 cm thick ..... *Matelea panamensis*
pp. Fruits ellipsoid to ovoid, woody or coriaceous, longitudinally 3–7 winged, less than 20 cm long, less than 5 cm thick.
q. Fruits ellipsoid, the walls distinctly woody, with 4 wings running the length of the fruit; ca. 8 cm long, 2 cm thick ..... *Cryptostegia madagascariensis*
qq. Fruits ellipsoid to ovoid, the walls thin and leathery, 3–7 winged; size various.
r. Fruit with one dorsal and 2 lateral wings running the full length of the fruit, attenuate-ellipsoid, at least 5 cm long, 1 cm wide; stems glabrous ..... *Gonolobus fuscoviolaceus*
rr. Fruits 5- or 7-winged, attenuate-ovoid, 7–11 cm long, 2–3 cm wide; stems glabrous or long brown pubescent.
s. Fruits with 2 full length lateral wings and a single dorsal wing ca. ¾ the length of the fruit, ca. 7–8 cm long, 2–3 cm wide, stems glabrous ..... *Matelea viridiflora*
ss. Fruits 7 winged, ca. 11 cm long, 3 cm thick; stems long, brown pubescent ..... *Matelea trianae*

oo. Fruits pubescent, with tuberculate projections.
  t. Fruit ellipsoid-attenuate, with long finger-like tubercles, the pubescence of long, brown, septate hairs, 10–15 cm long, 2–3 cm wide ... *Matelea pinguifolia*
  tt. Fruit ellipsoid, not attenuate, with short tubercles capped with light-colored corky tissue, the pubescence short, gray, nonseptate, ca. 8 cm long, 3 cm wide ... *Matelea maritima*

1. CRYPTOSTEGIA

Cryptostegia R. Br., Bot. Reg. *t.* 435. 1820. TYPE: *C. grandiflora* (Roxb.) R. Br.

Glabrous *vines* or climbing *shrubs*; stems woody, glabrous with conspicuous lenticels; sap copious, milky. *Leaves* short petiolate, coriaceous, lanceolate to nearly orbicular, basally rounded, apically short acuminate, dark shiny green above, paler beneath with conspicuous fine reticulate veins. *Inflorescence* several-flowered, cymose, terminal. *Flowers* with the calyx 5-lobed, cleft to the base, the lobes ovate to lanceolate, acute; corolla whitish, pink, or lavender, funnelform, the lobes greatly exceeding the tube, usually recurved when fully open; true corona absent, but with 5 corolline appendages on the tube, subulate, or bisected into filiform lobes, stamens short, mounted on the base of the corolla, anthers and filaments distinct, not joined into a single unit; pollen distinct as tetrads, not agglutinated into pollinia; pistils joined at base and apex, stigma large, globular. *Fruit* a single ± boat-shaped follicle, woody with ribs or wings traversing the long axis; seeds numerous, small, comose.

There are 2 species of *Cryptostegia*, one native to Madagascar, the other to India. Both are widely planted for ornament, but the name *C. grandiflora* is often mistakenly applied to both.

The subfamily Periplocoideae, of which *Cryptostegia* is a member, is an interesting Old World assemblage of about two dozen genera. There is good evidence, both morphological and anatomical, for segregating the group as a distinct family, Periplocaceae.

1. **Cryptostegia madagascariensis** Bojer *ex* Dcne. *in* DC., Prod. 8: 492. 1844. TYPE: Madagascar, *Bojer* (P?, not seen).—FIG. 1.

Glabrous woody *vines* or climbing *shrubs*; stems with prominent lenticels on younger wood, copiously lactiferous. *Leaves* glabrous, ovate, apically acuminate, basally rounded to obtuse, finally tapering to the short petiole; the blades 4–10 cm long and 3–5 cm broad; petiole ca. 7 mm long, shiny on the upper surface, finely and prominently reticulate beneath. *Inflorescence* a loose terminal cyme, few- to several-flowered. *Flowers* with the calyx lobes broadly lanceolate, acuminate, the margins ± chartaceous, 8–9 mm long and 4–6 mm wide; corolla pinkish to purplish, funnelform, the tube 1.5–2.5 cm long, puberulent outside, the lobes ovate, 2.4–3.0 cm long, reflexed at anthesis; gynostegium ca. 5 mm high,

→

FIGURE 1. *Cryptostegia madagscariensis* Bojer *ex* Dcne.—A. Flowering stem (× 3/5).—B. Opened floral tube showing corona segments (× 1½).—C. Fruit (× 3/5). [After *Tyson* 5599 (MO).]

C
B
A
RJWhite

the stamens not united but lightly coherent; corona corolline, the 5 distinct subulate segments each 8–9 mm long, and attached to the corolla tube; pollen granular. *Fruit* woody, ca. 8 cm long and 2–3 cm wide, exocarp with a single dorsal and 2 lateral wings; seeds small, comose.

Native to Madagascar, this species is widely used as an ornamental. The copious latex is reported to cause varying degrees of skin irritation. *Cryptostegia madagascariensis* is, at least in the herbarium, often mistakenly identified as *C. grandiflora* R. Br. This latter taxon is probably grown in Panama, but no specimens have been seen. It is readily distinguished by its larger flowers and fruits, and by the corona segments which are bifurcately split into filiform lobes. *Cryptostegia grandiflora* yields a reasonably high quantity of rubber from its latex, and it was formerly used commercially for that purpose hence its common name "India rubber vine."

CANAL ZONE: Plant introduction garden at Summit, *Steyermark* 1935 (MO). Curundu, *Tyson 5048* (MO). HERRERA: 1 mi. E of Chitré near airport, *D'Arcy & Croat 4188* (MO). PANAMÁ: Saboga Island, in village, *Tyson* 5599 (MO).

2. ASCLEPIAS

Asclepias L., Sp. Pl. 214. 1753; Gen. Pl., ed. 5. 123. 1754. TYPE: *A. syriaca* L.

Perennial or rarely annual *herbs*, usually erect, glabrous or pubescent. *Leaves* opposite or verticillate. *Inflorescences* umbellate, many-flowered. *Flowers* variously colored, but generally whitish or purplish; calyx 5-lobed, usually with 5–10 glandular structures at the bases of the sinuses; corolla rotate or reflexed at maturity, deeply 5-lobed, the lobes glabrous within, valvate in bud; corona of 5 usually cucullate segments which are joined to the corolla tube, each segment usually with a ligulate "horn" within, the filaments connate into a tube, the anthers terminated by an inflexed membrane; pollinia oblong, pendulous in the anther thecae; stigma pentagonal or 5-lobed, apically flattened. *Follicles* usually thickened, acuminate, the exocarp usually smooth or sometimes spinose-tuberculate; seeds comose.

A large genus centered principally in temperate North and South America, *Asclepias* is represented by about 10 species in Central America and by one species in Panama. The diminutive and infrequently collected *Asclepias woodsoniana* Standl. & Steyermark is to be expected along the Pacific coast of the Republic, as it is known from the savannas of Honduras, Costa Rica, and Colombia. It is a green-flowered, small herb, known from grasslands.

1. **Asclepias curassavica** L., Sp. Pl. 215. 1753.—FIG. 2.

Erect *herb*, 60–80(–200) cm high, mostly simple- but sometimes multi-stemmed, green, glabrous or slightly pubescent on the younger parts. *Leaves* opposite, lanceolate to linear-lanceolate, attenuate-acuminate, basally acute or attenuate, 5–16 cm long and 1–4 cm wide; blades thin, glabrous or glabrate; petioles 1–2 cm long. *Inflorescence* few-flowered, axillary; pedicels 1–2 cm long,

FIGURE 2. *Asclepias curassavica* L.—A. Flowering stem (× 3/5).—B. Flower (× 2 2/5). [After *Lewis et al.* 2937 (MO).]—C. Follicles (× 3/5). [After *Dodge & Allen 17486* (MO).]

puberulent. *Flowers* with the calyx green, hidden by the reflexed petals in the mature flower, 5-lobed, the lobes 2–3 mm long and 0.8–1 mm wide; corolla red to orange-red, lobes ovate to oblong, 4–7 mm long and 2–3 mm wide; corona segments erect, broadly ovate, 4–5 mm long, rounded or obtuse at the apex, exceeded by the conspicuous inner horns, bright yellow. *Follicles* erect, fusiform, slender, 8–10 cm long, 1–1.5 cm in diameter; seeds ca. 6 mm long, narrowly winged, with a white, silky coma.

A widely distributed weedy species ranging from Florida to South America and the West Indies, it is known from all provinces of Panama. "Niño Muerto" (Standley).

BOCAS DEL TORO: Changuinola Valley, *Dunlap 316* (US). Along runway at Bocas, *Lazor & Tyson 2382* (FSU). Bocas del Toro, *Carleton 177* (US); *Wedel 385* (MO). Near Chiriqui Lagoon, *Wedel 1252* (MO). Isla Colón, *Wedel 574, 2795* (both MO). Fish Creek Hills, *Wedel 2461* (MO). Water Valley, *Wedel 656* (MO). CANAL ZONE: Barro Colorado Island, *Croat 6339, 6374, 7299, 8245* (all MO); *Ebinger 639* (MO, US); *Luteyn 722* (DUKE); *Shattuck 169* (MO, US); *Standley 31245* (US). Cerro de Ancón, *Celestine 56* (US); *Hladik 356* (MO, US); *Killip 3037* (MO, US). Pipeline road near Gamboa, *Clewell & Tyson 3319* (MO); *Wilbur & Weaver 11268* (DUKE). Madden Dam & along Azote Caballo Road near Alahuela, *Dodge 16622* (MO). Between Río Indio Hydrographic Station and Natural Bridge at Río Puente, *Dodge & Allen 17486* (MO). Near Gatun Locks, *Dwyer 1790* (FSU). Hills W of Canal near Gatún, *Standley 27290* (US). Near Arraijan, *Dwyer et al. 4347* (MO). Chagres, *Fendler 258* (MO, US). Balboa Heights, *Greenman & Greenman 5061* (MO). Las Cruces Trail, *Hunter & Allen 679* (MO); *Standley 29212* (US). Fort San Lorenzo, Fort Sherman Military Reservation, *Maxon & Valentine 7008* (US). Chiva-Chiva Trail, Red Tank to Pueblo Nuevo, *Piper 5709* (US). Near Fort Randolph, *Standley 28743* (US). Río Pedro Miguel near E. Paraiso, *Standley 30033* (US). Near Miraflores Lake, *White & White 193* (MO). Between France Field, CZ, & Cativa1, Prov. of Colón, *Standley 30289* (US). CHIRIQUÍ: Roadside W of Cerro Pando, *D'Arcy & D'Arcy 6633* (MO). Boquete District, Bajo Mono, *Davidson 470* (MO). Near Boquete, *Lewis et al. 623* (MO, US); *Pittier 2947* (US). Finca Lerida to Boquete, *Woodson et al. 1127* (MO). COCLÉ: El Cope, *Tyson 5200* (DUKE, FSU, MO). ½ mi. from El Cope, *Correa 401* (DUKE, MO). Road to El Cope from Interamerican Highway, *Burch et al. 1383* (MO). 12 mi. NE of Penonomé, *Lewis et al. 1518* (F, MO). Boca del Toabré at confluence of Río Toabré & Río Coclé del Norte, *Lewis et al. 5505* (MO). El Valle de Antón, *Seibert 445* (MO); *Wilbur & Luteyn 11718* (DUKE). 7 mi. N of El Valle de Antón, *Luteyn 1219* (DUKE). COLÓN: Near Colón, *Lehmann 990* (US). Old Experiment Station, 3 mi. E of Panama City, *Maxon et al. 2089* (US). Road to San Lorenzo, *Quistgaard 11* (MO). DARIÉN: Ca. 10 mi. S of El Real on Río Pirre, *Duke 5422* (MO). Boca Yaviza, *Duke 8360* (OS). Río Tuira, between Río Punusa and Río Mangle, *Duke 14593* (MO). Trail between El Real and Pinogana, *Stern et al. 273* (MO, US). HERRERA: Road from Chitré to Divisa, *Burch et al. 1351* (MO, US). 4 mi. S of Los Pozos, *Tyson 2662* (FSU, MO). LOS SANTOS: Río Tonosí, near Tonosí, *Lewis et al. 1564* (F, MO). Headwaters of Río Pedregal, 25 mi. SW of Tonosí, *Lewis et al. 2937* (F, MO). Punta Mala, near mouth of Río Caldera, *Tyson 2734* (MO). PANAMÁ: Near Chepo, *Dodge 10718* (MO); *Hunter & Allen 31* (MO). Interamerican Highway E of Bejuco, *Duke 4550* (MO). Near El Llano, *Duke 5840* (MO). Río Pacora just below Río Corso, *Duke 11987* (MO). Río Tocumen, N of Chepo Road, *Hunter & Allen 216* (MO). Near Tapia River, Juan Diaz Region, *Maxon & Harvey 6670, 6718* (both US). Río Tapia, *Standley 28132* (US). 1 mi. N of Goofy Lake, *Oliver et al. 2676* (MO). Near big swamp E of Río Tocumen, *Standley 26628* (US). Río Tocumen, *Standley 26737* (US). Los Asientos, *Wendehake 25* (DUKE, MO). Hills above Campana, *Allen 1211* (MO). Cerro Campana, 8.6 mi. SW of Capira, *Luteyn 1034* (DUKE). Cerro Jefe, *Duke 9402* (OS); *Wilbur & Weaver 11352* (DUKE). SAN BLAS: Sasardí, *Duke 10125* (MO, OS). Road between Mandinga and Cangandí, *Duke 14752* (MO). Headwaters of Río Mulatupo, *Elias 1754* (MO). VERAGUAS: Santiago, 4 mi. from Transisthmian Highway to Atalaya, *Dwyer & Kirkbride 7407* (MO). 1–2 mi. above Sante Fé, *Gentry 3056* (MO). Road between Laguna La Yeguada and Calobre, *Luteyn 1476* (DUKE). Puerto Mutis, 12 mi. S of Santiago, *Tyson 5189* (FSU).

3. CALOTROPIS

Calotropis R. Br., Mem. Wern. Soc. 1: 39. 1809. LECTOYPE: *Calotropis procera* (Ait.) Ait. f.

Large coarse *herbs* sometimes becoming shrubby with age. *Leaves* sessile or nearly so, broad and somewhat fleshy. *Inflorescences* umbelliform or racemiform cymes. *Flowers* with the calyx deeply 5-lobed, the lobes lanceolate to ovate; corolla shallowly campanulate, apices of the lobes usually purple, triangular-ovate, cut halfway to the base or less, valvate in bud; stamens adnate near the base of the corolla, corona of 5 fleshy segments adnate to the staminal column and with an upcurved spur and auricles at the base. *Fruit* usually a pair of inflated, fleshy, follicles.

An Old World genus of 2 species, the following and *C. gigantea* (L.) Ait., restricted to Asia and Africa. The species treated here is now pantropical in distribution.

1. **Calotropis procera** (Ait.) Ait. f., Hort. Kew., ed. 2. 2: 78. 1811.—FIG. 3.

Asclepias procera Ait., Hort. Kew., ed. 1. 2: 305. 1789. TYPE: (not seen).

Coarse erect *herbs* or *subshrubs* to 2 m or more high; stems glaucous, with age developing thick corky, deeply furrowed bark. *Leaves* glaucous, ovate to nearly orbicular, sessile or nearly so, apically acute, basally cordate, 10–30 cm long and 8–20 cm broad. *Inflorescences* branched umbelliform cymes, many flowered. *Flowers* with calyx lobes ovate-triangular, 5–6 mm long and 3–4 mm wide; corolla shallowly campanulate to nearly rotate, ca. 2.5 cm in diameter, lobed to about the middle, the lobes triangular, 9–11 mm long and 7–9 mm wide, greenish outside, whitish inside with the lobes usually purple tipped. *Follicles* short and broad, 5–7 cm long and 3–4 cm wide.

Native to Asia, *C. procera* has long been naturalized in the West Indies and along the east coast of South America. Relatively few collections have been seen from Central America, these from Guatemala, Honduras, El Salvador, and Panama. The fruits are reputedly extremely toxic.

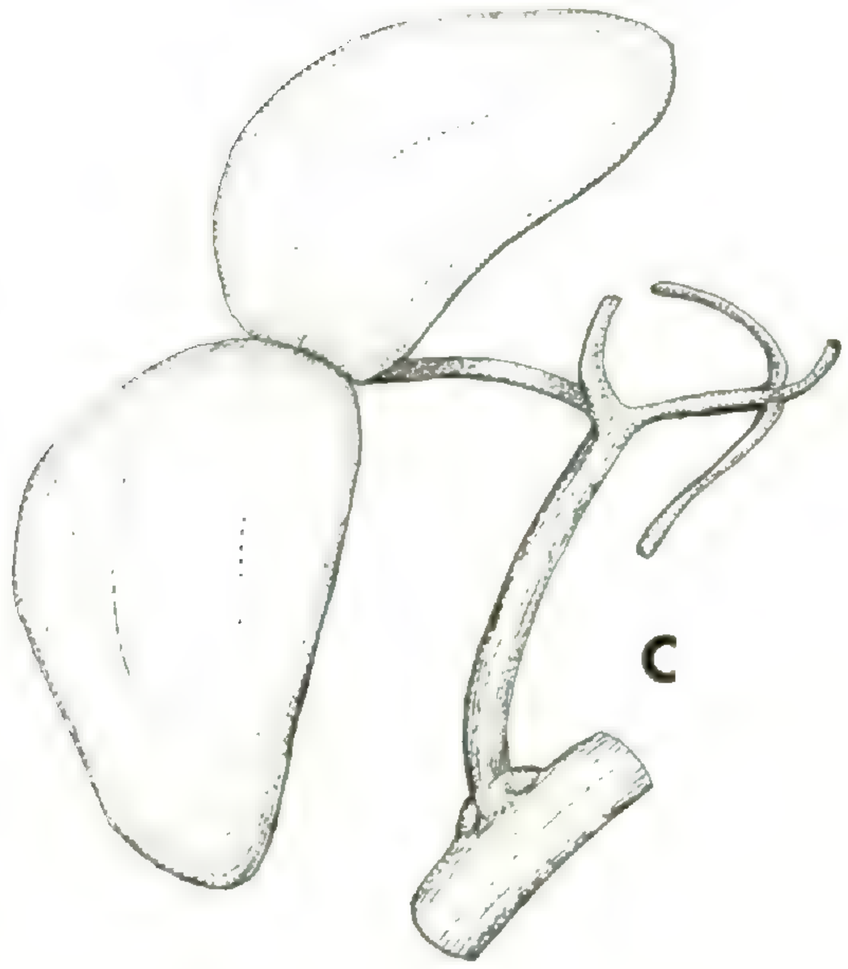
LOS SANTOS: Monagre Beach road, ca. 5 mi. SE of Los Santos, *Lewis et al. 1683* (F, MO). PANAMÁ: Taboga Island, *D'Arcy & D'Arcy 6802* (MO).

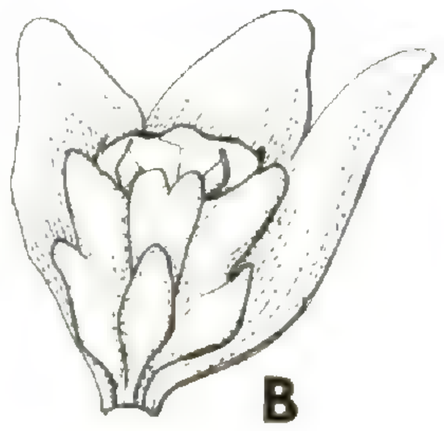
4. OXYPETALUM

Oxypetalum R. Br., Mem. Wern. Soc. 1: 41. 1809, *nomen conserv.* TYPE: *O. banksii* J. A. Schultes.

Gothofreda Vent., Choix Pl. Cels. 7, 5. 60. 1803, *nomen rej.* TYPE: *G. cordifolia* Vent.

Mostly scandent *herbs*, occasionally suffrutescent, usually pubescent. *Leaves* opposite, generally cordate and long petiolate. *Cymes* usually umbellate, terminal or axillary, few- to several-flowered. *Flowers* with the calyx 5-lobed, with or without basal interior glands; corolla usually white, yellow, or purplish, campanulate to subglobose, the tube short, deeply 5-lobed, the lobes usually narrow, contorted in bud; stamens inserted near the base of the tube, the corona 5-parted,





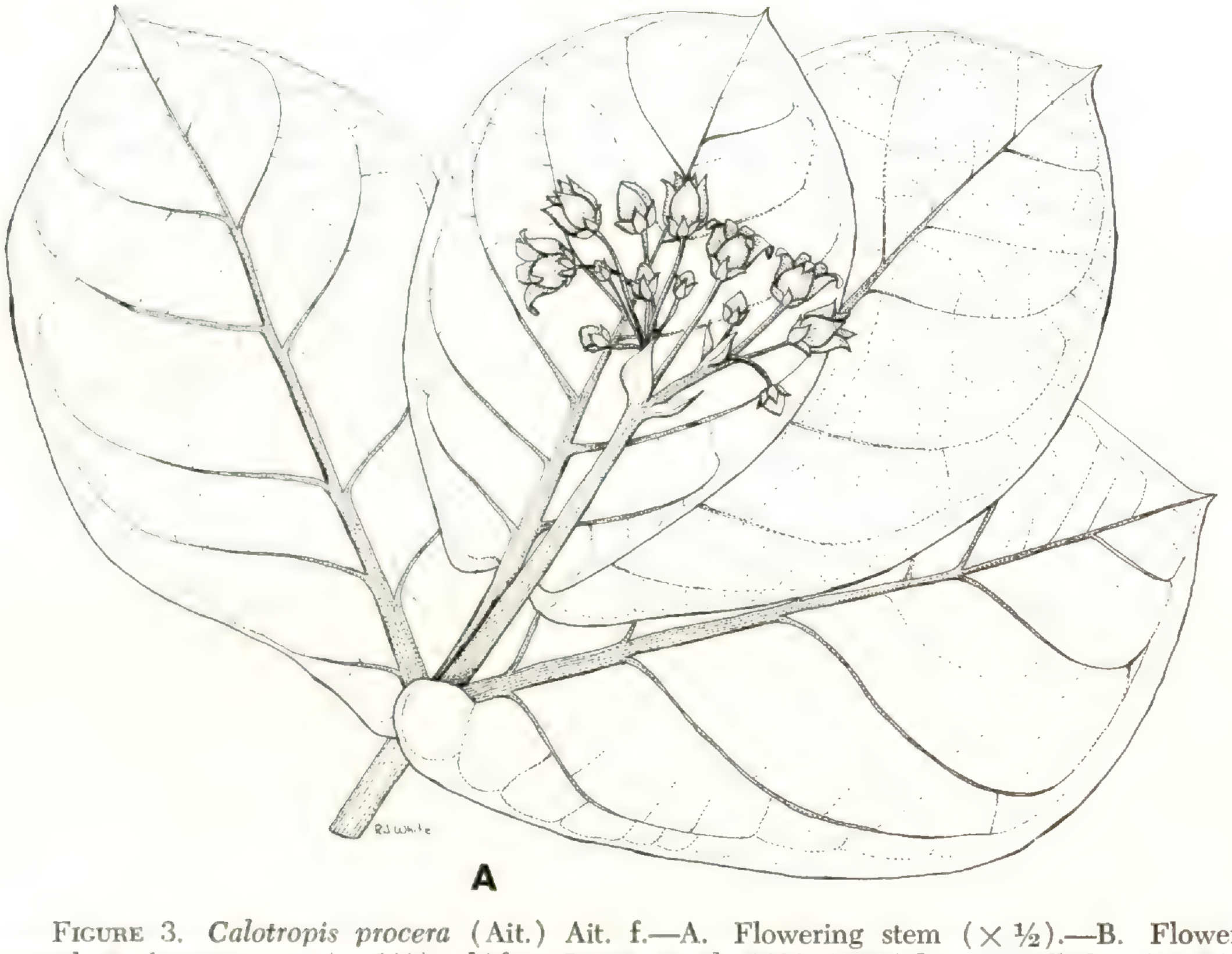


Figure 3. *Calotropis procera* (Ait.) Ait. f.—A. Flowering stem (× ½).—B. Flower opened to show corona (× 1½). [After *Lewis et al. 1683* (MO).]—C. Follicles (× ⅗). [After *Harmon & Fuentes 2135* (MO).]

adnate to the corolla or free, erect, the segments usually fleshy, ± retuse, emarginate or bifid, with or without interior appendages, the filaments forming a short tube, the anthers terminated by an inflexed membrane; pollinia pendulous, usually oblong, translators usually with strongly appendaged dorsal margins; stigma usually beaked, the beak frequently bifid. *Follicles* slender or thickened, smooth or tuberculate; seeds comose.

A New World genus of 80–100 species, all but one of which are now known only from South America.

1. **Oxypetalum cordifolium** (Vent.) Schltr. *in* Urban, Symb. Antill. 1: 269. 1899.—Fig. 4.

Gothofreda cordifolia Vent., Choix Pl. Cels. 7, 5. 60. 1803. TYPE: (not seen).
Oxypetalum riparium H.B.K., Nov. Gen. Sp. Pl. 3: 197. 1819. TYPE: (not seen).

Slender herbaceous *vines*, sometimes somewhat woody, finely velutinous-pilosulous on the stems, leaves, and inflorescences. *Leaves* soft, membranaceous, ovate, cordate, acuminate or cuspidate at the apex, dark green above, paler beneath, mostly 5–10 cm long and 4–6 cm wide; the petiole slender, 3–5 cm long. *Cymes* umbellate, 1- or few-flowered; peduncles ca. 2 cm long; pedicels slender, 1–1.5 cm long. *Flowers* with the calyx deeply lobed, the lobes linear-lanceolate to linear-subulate, densely pubescent on the outside, ca. 3.5 mm long and 0.5 mm wide; corolla yellowish to greenish, puberulent outside, glabrous to minutely papillose inside, the short tube ca. 4 mm long, the lobes linear attenuate, 1.5–2.5 cm long, ascending or spreading; corona 5-parted, the segments somewhat thickened, truncate-spathulate, the apex ± plicate, each bearing a small appendage on the inner face, basally connate with the staminal tube, ca. 3 mm long; stigma terminating in a conspicuous bifid, 3–4-mm-long beak. *Follicles* ca. 11 cm long, fusiform with a long acuminate apex.

Ranging from Mexico to the West Indies and through Central America into northern South America, *Oxypetalum cordifolium* is known from a single locality in Panama.

PANAMÁ: Cerro Campana, 800 ft, *Allen 3974* (MO). Cerro Campana, 2000 ft, *Tyson 6437* (MO, FSU).

5. CYNANCHUM[4]

Cynanchum L., Sp. Pl. 212. 1753; Gen. Pl., ed. 5. 123. 1754. TYPE: *C. acutum* L.

Metastelma R. Br., Mem. Wern. Soc. 1: 52. 1809. TYPE: *M. parviflora* (Sw.) R. Br. *ex* Schultes.
Tassadia Dcne. *in* DC., Prod. 8: 579. 1844. TYPE: (not seen).
Metalepis Griseb., Cat. Pl. Cub. 179. 1866. TYPE: *M. cubensis* (A. Rich.) Griseb.

Usually scandent *herbs*, sometimes suffrutescent, glabrous or pubescent. *Leaves* opposite, coriaceous to membranaceous, frequently small and narrow. *Inflorescences* umbelliform or racemiform, sessile or pedunculate. *Flowers* with the calyx deeply 5-lobed, generally 5-glandular at the base within, the lobes often obtuse and small; corolla mostly whitish or yellowish, occasionally pink to brownish-purple, urceolate to campanulate to subrotate, usually small, 5-lobate, the lobes often pubescent within; stamens 5, the corona mostly of 5 distinct or connate segments, laminate to filiform, sometimes fleshy and minute, rarely absent, sometimes variously compound or with internal processes, the filaments

[4] Only those synonyms applying to Panamanian species are included here. A more extensive list is found in Woodson (1941).

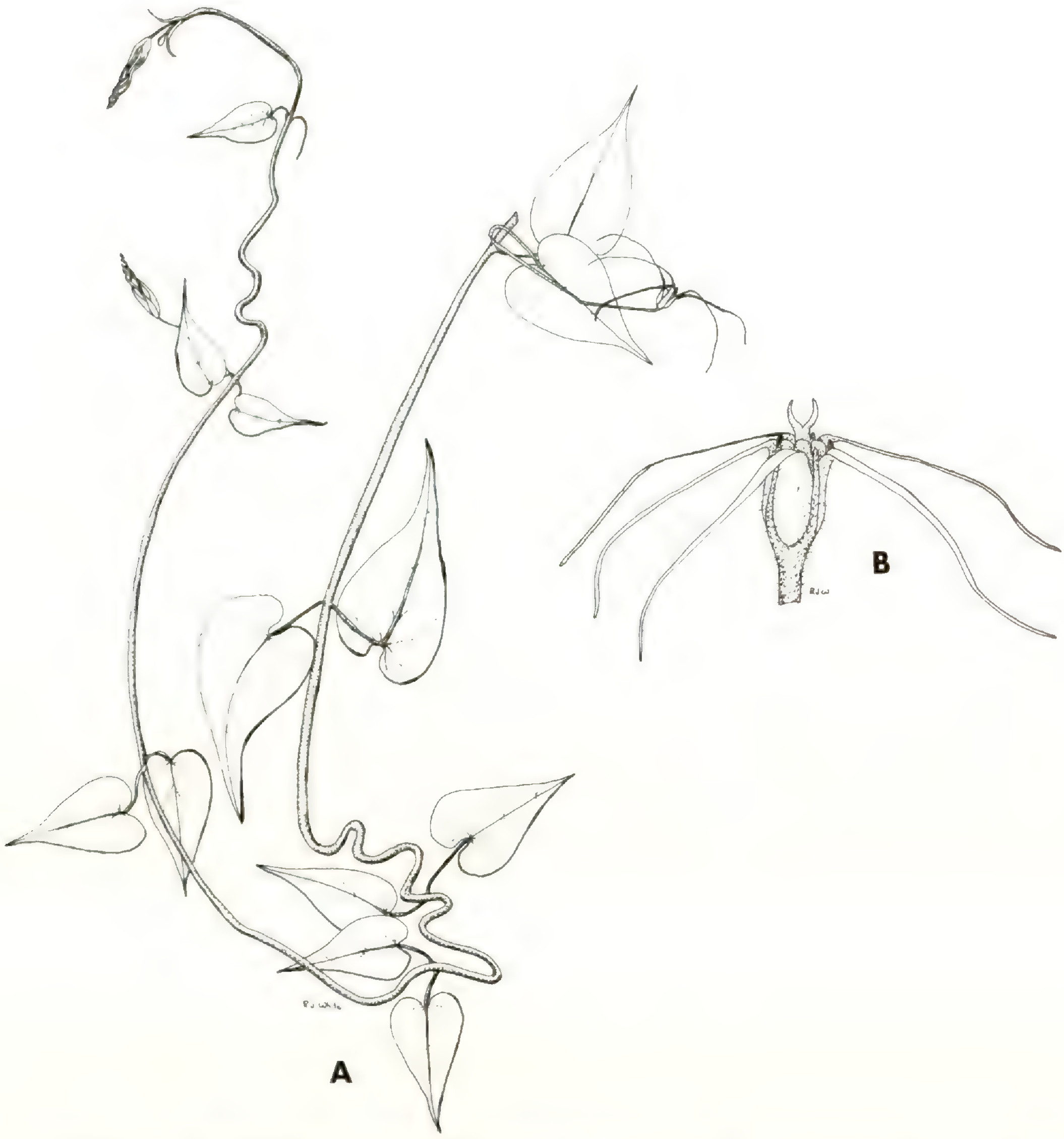


FIGURE 4. *Oxypetalum cordifolium* (Vent.) Schltr.—A. Flowering stem (× ½).—B. Flower (× 1½). [After *Tyson 6437* (MO).]

connate into a short to elongate tube, the anthers terminated by an inflexed membrane; pollinia usually ovoid or oblong, pendulous; stigma apically flat or variously elaborated into a beak. *Fruit* single or paired follicles, smooth, usually terete or nearly so, commonly slender and acuminate, sometimes ovoid.

A large genus, which, when considered in the wide sense, includes in excess of 200 species. These are widely distributed throughout temperate and tropical regions of both hemispheres.

a. Leaves basally cordate; flowers large, the petals 2.5 mm long or more; follicles large, not paired.
   b. Inflorescence racemose; corolla lobes glabrous inside, more than 6 mm long (subgenus *Roulinia*) ..... 6. *C. magdalenicum*

bb. Inflorescence paniculate; corolla lobes white pubescent inside, 3.5 mm long or less (subgenus *Metalepis*) ..... 5. *C. cubense*

aa. Leaves not cordate; flowers small, the petals less than 2 mm long; follicles small, usually paired.

c. Leaves thick, dark shiny green above, paler beneath; umbels in spreading racemiform inflorescences (subgenus *Tassadia*).

d. Sepals equaling or exceeding the corolla tube in length ..... 1. *C. recurvum*

dd. Sepals shorter than the corolla tube ..... 2. *C. apocynellum*

cc. Leaves thin, uniformly colored above and beneath; simple unbranched umbelliform inflorescences (subgenus *Metastelma*).

e. Corolla lobes glabrous inside; corona segments ovate-oblong, overtopping the gynostegium ..... 3. *C. glaberrimum*

ee. Corolla lobes pubescent inside; corona segments subulate, equaling the gynostegium ..... *C. infimicola*

1. **Cynanchum apocynellum** (Gl. & Mold.) Spellman, Phytologia 25: 438. 1973.

Tassadia apocynella Gl. & Mold. *ex* Mold., Phytologia 1: 15. 1933. TYPE: Colombia, *Lawrance 584* (NY, MO).

Slender herbaceous *vines*, minutely and sparingly scabrous on the stems, petioles, and inflorescence. *Leaves* rhombic-elliptic, basally cuneate, apically acuminate, the margins revolute at least in drying, mostly 4.5–4.8 cm long and 2.3–2.8 cm wide, glabrous beneath, sparsely appressed pubescent above, more densely so along the midrib, with 1–3 short broad glands at the base of the upper surface; petioles 8–13 mm long. *Inflorescence* a panicle of sessile, 3–5-flowered umbels; pedicels 2.5–3.0 mm long, densely short pubescent. *Flowers* with the calyx conspicuously shorter than the corolla tube, minutely pubescent outside, glabrous within, a single dactyliform gland within at the base of each sinus, the lobes 0.6–0.7 mm long and ca. 0.4–0.6 mm wide, ovate, obtuse; corolla urceolate, the tube 0.9–1.1 mm long, nearly as broad, glabrous, the 5 lobes recurved for about half their length, lanceolate-ovate, densely white papillose inside, 1.9–2.1 mm long and ca. 1.0 mm wide; corona segments 5, apparently distinct, helmet-shaped in outline, ca. 0.75 mm broad and ca. 0.4 mm high; gynostegium short, conical, broad at the base, truncate, ca. 0.6–0.7 mm high. *Follicles* generally paired, 3.5–3.8 cm long, slender, apically long attenuate.

This species is known only from Colombia and from a single locality in Panama.

PANAMÁ: 1 mi. despues de la Eneida cerca de Cerro Jefe, *Correa & Dressler 969* (MO). Cerro Jefe, *Duke 9444* (MO, OS).

2. **Cynanchum recurvum** (Rusby) Spellman, Phytologia 25: 438. 1973.

Tassadia recurva Rusby, New Sp. S. Amer. Pl. 97. 1920. TYPE: Colombia, *Smith 1621* (MO, NY).

Herbaceous *vines*, young stems pubescent, glabrescent. *Leaves* thick, dark green above, lighter beneath, the margins revolute at least when dry, lanceolate to elliptic, basally obtuse to rounded, apically rounded, apiculate, sparingly pubescent with short white, closely appressed hairs above, glabrate beneath, mostly 3.5–5.5 cm long and 2.0–2.6 mm wide with a pair of glands at the base; petioles 4–8 mm long, pilose. *Inflorescence* a panicle of umbels to ca. 15 cm long,

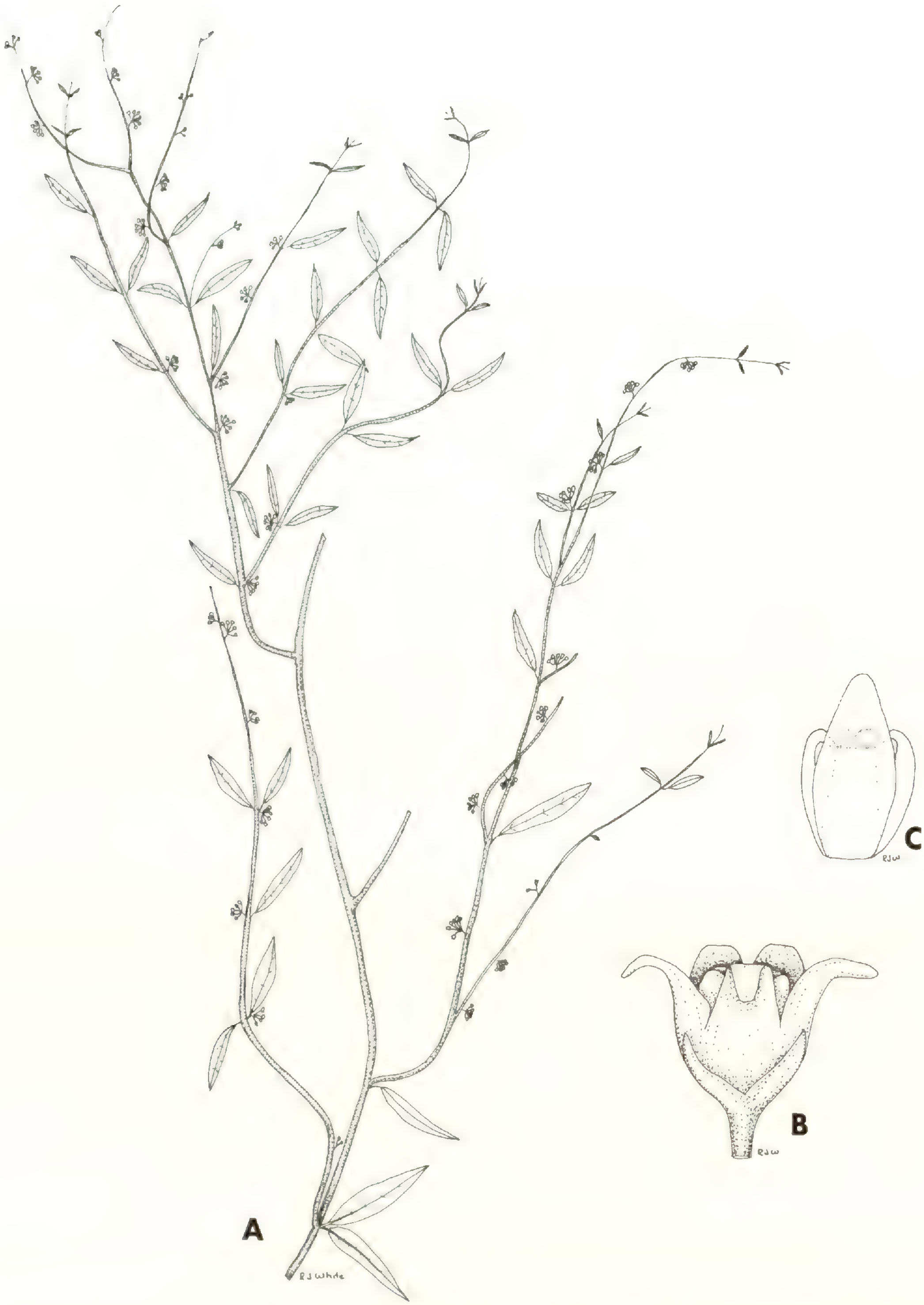


FIGURE 5. *Cynanchum glaberrimum* (Woodson) L. O. Wms.—A. Flowering stem (× 3/5). —B. Flower (× 6).—C. Corona with one lobe expanded (× 1/6). [After *Woodson & Schery* 233 (MO).]

umbels 3–5-flowered, inflorescence branches and pedicels pubescent; pedicels slender, 2–4 mm long. *Flowers* with the calyx equaling or exceeding the corolla tube, the lobes 0.7–0.8 mm long and about as wide, ovate, pubescent outside with 1 or 2 flattened glands on the interior in each sinus; corolla yellow-green, campanulate, the tube ca. 7 mm long and ca. 1.5 mm wide at the throat, the lobes spreading or reflexed, lanceolate-ovate, densely white papillose inside, glabrous outside, 1.2–1.8 mm long and 0.8–0.9 mm wide; corona ± fleshy, greenish-white, composed of 5 transversely depressed lobes opposite each stamen and a rounded cupped portion between each lobe, ca. 0.2 mm high; gynostegium truncate-conical, exserted from the corolla, 0.7–0.8 mm high. *Follicles* unknown.

This species is known from northern South America with single collections from Panama and Costa Rica.

Both this species and the preceding one belong to a small tightly knit complex of 6 or 8 species. The group is difficult primarily because of the small flowers. Critical study may reveal that the group merits generic status.

CANAL ZONE: Barro Colorado Island, 200 m N of Zetek trail above the escarpment, *Croat 15000* (MO).

3. **Cynanchum glaberrimum** (Woodson) L. O. Wms., Fieldiana: Bot. 32: 36. 1968.—FIG. 5.

Metastelma glaberrimum Woodson, Ann. Missouri Bot. Gard. 24: 200. 1937. TYPE: Panama, *Seibert 300* (MO).

Slender suffruticose *vines*, the stems somewhat compressed and corky, glabrous or nearly so except on younger growth. *Leaves* elliptic to lanceolate-ovate to ovate, acuminate, glabrous; petioles 2–5 mm long, glabrous or puberulent; the blades mostly ca. 2.5 cm long and 0.4–1.5 cm wide, 2 small glands present at the base. *Cymes* axillary, umbelliform, puberulent, few-flowered; peduncle 1–3 mm long; pedicels 1–3 mm long. *Flowers* with the calyx divided to the base, the lobes ovate, obtuse, ca. 0.8 mm long; corolla whitish, campanulate, the tube 0.5–0.8 mm long, the lobes glabrous, 1–1.5 mm long and ca. 0.6 mm wide; corona segments widely ovate, 0.6–0.9 mm long; gynostegium truncate-conical, ca. 0.5 mm high. *Follicles* unknown.

Said to be common in Costa Rica, the species is also known from Colombia. It is known from only one province in Panama.

CHIRIQUÍ: Near Monte Lirio, valley of the upper Río Chiriquí Viejo, *Seibert 300* (MO). Near Casita Alta, Volcán de Chiriquí, *Woodson et al. 923* (MO). Río Chiriquí Viejo Valley, along river on island, *White 152* (MO). Near Finca Lerida, *Woodson & Schery 233* (MO, US).

4. **Cynanchum infimicola** L. O. Wms., Ann. Missouri Bot. Gard. 55: 48. 1968. TYPE: Panama, *Dwyer & Hayden 7540* (F, MO).

Slender herbaceous *vines*; stems mostly less than 1 mm in diameter, pubescent in lines with one or more small glands on the interpetiolar scars. *Leaves* lanceolate to narrowly ovate, acuminate, glabrous or nearly so, 1.5–4.5 cm long and 0.8–2.0 cm wide; the slender petioles 3–9 mm long, pubescent. *Cymes* umbelli-

form; peduncles slender, mostly 6–10 mm long, pubescent, few- to many-flowered; pedicels 2 mm long or less. *Flowers* with the calyx deeply 5-parted, the lobes elliptic to lanceolate, ca. 0.7 mm long, sparsely puberulent to glabrous; corolla campanulate to suburceolate, the tube ca. 0.7 mm long, glabrous, lobes lanceolate, acute, slightly spreading, densely puberulent within, ca. 1.5 mm long and ca. 0.5 mm wide; corona segments subulate, ca. 1.4 mm long; gynostegium ca. 1.3 mm high; the stigma flat. *Follicles* paired, subfusiform, smooth, glabrous, 4.4–5 cm long, 3–4 mm in diameter.

This species is endemic to the Pacific lowlands of Panama.

CANAL ZONE: K-2 Road, *Dwyer & Hayden 7540* (MO). Farfan Beach and vicinity, *Dwyer et al. 540* (MO); *Kirkbride & Elias 57* (MO); *Tyson 1817* (FSU, MO). COCLÉ: Road to El Cope ca. 7 mi. from Interamerican Highway, *Correa 403* (DUKE, MO). Aguadulce along outskirts of tidal belt, *Pittier 4999* (US). Ca. 2 mi. W of El Valle de Antón, *Luteyn 1252* (DUKE, MO). Between Las Margaritas and El Valle, *Woodson et al. 1263* (MO). Road to El Valle de Antón, *D'Arcy & D'Arcy 6717* (MO). PANAMÁ: Isla Tabaguilla, *Duke 5871* (MO). Morro Island (off Tobago), *D'Arcy & D'Arcy 6780* (MO). Isla de Tobago, *Dwyer 2809* (MO); *Pittier 3539* (US); *Woodson et al. 1499, 1500, 1501* (all MO). Río Mar, along road to beach, *Blum & Dwyer 2485* (FSU, MO). Savanna near Río Mar, *Duke 12414* (MO, OS). Near beach at Nueva Gorgona, *Duke 4491* (MO).

5. **Cynanchum cubense** (A. Rich.) Woodson, Ann. Missouri Bot. Gard. 28: 213. 1941.—FIG. 6.

Gonolobus cubensis A. Rich., Fl. Cub. Fanerog. 2: 98. 1845. TYPE: Cuba, *Valenzuela* (P, not seen).
Metalepis cubensis (A. Rich.) Griseb., Cat. Pl. Cub. 180. 1866.
Cynanchum peraffine Woodson, Ann. Missouri Bot. Gard. 31: 236. 1944. TYPE: Mexico, *Calderone 258* (GH, US).

Large herbaceous *vines* with abundant latex, the stems glabrous or nearly so, hollow. *Leaves* widely ovate, deeply cordate when mature, or shallowly cordate, apically acuminate to short-apiculate, glabrous, 10–30 cm long and 7–19 cm wide with a cluster of laminar glands at the base; petioles 5–12 cm long, glabrate. *Inflorescence* at first racemose, branching to become a panicle of racemes to 30 cm long, the branches minutely puberulent, densely so when younger; pedicels mostly 2–4 mm long. *Flowers* with the calyx deeply lobed, the lobes shorter than the corolla lobes, ovate-lanceolate, acuminate, puberulent to glabrate on the outside, 1.5–3.0 mm long and 1.0–1.4 mm wide; corolla greenish-white, rotate, the lobes at anthesis reflexed, with revolute margins, glabrous outside, densely white papillose inside, 3.0–3.3 mm long and 1.3–1.4 mm wide; corona cyathiform, shallowly 5-lobed, shorter than the gynostegium, the lobes truncate with slightly inrolled lateral margins, ca. 0.6 mm long, glabrous to densely papillate inside; gynostegium 1.8–2.2 mm high, the column densely papillate, the head 2.4–2.7 mm in diameter, slightly umbonate. *Follicles* (described from Cuban material) ovate-oblong, smooth, 15–21 cm long, 7–10 cm in diameter.

This species occurs in Cuba, Panama, Colombia and Mexico.

The subgenus *Metalepis* is a highly variable and difficult group. As treated here, those plants having calyx lobes equal to or shorter than the corolla lobes are considered as *C. cubense*. I recognize two additional taxa, *C. albiflorum*

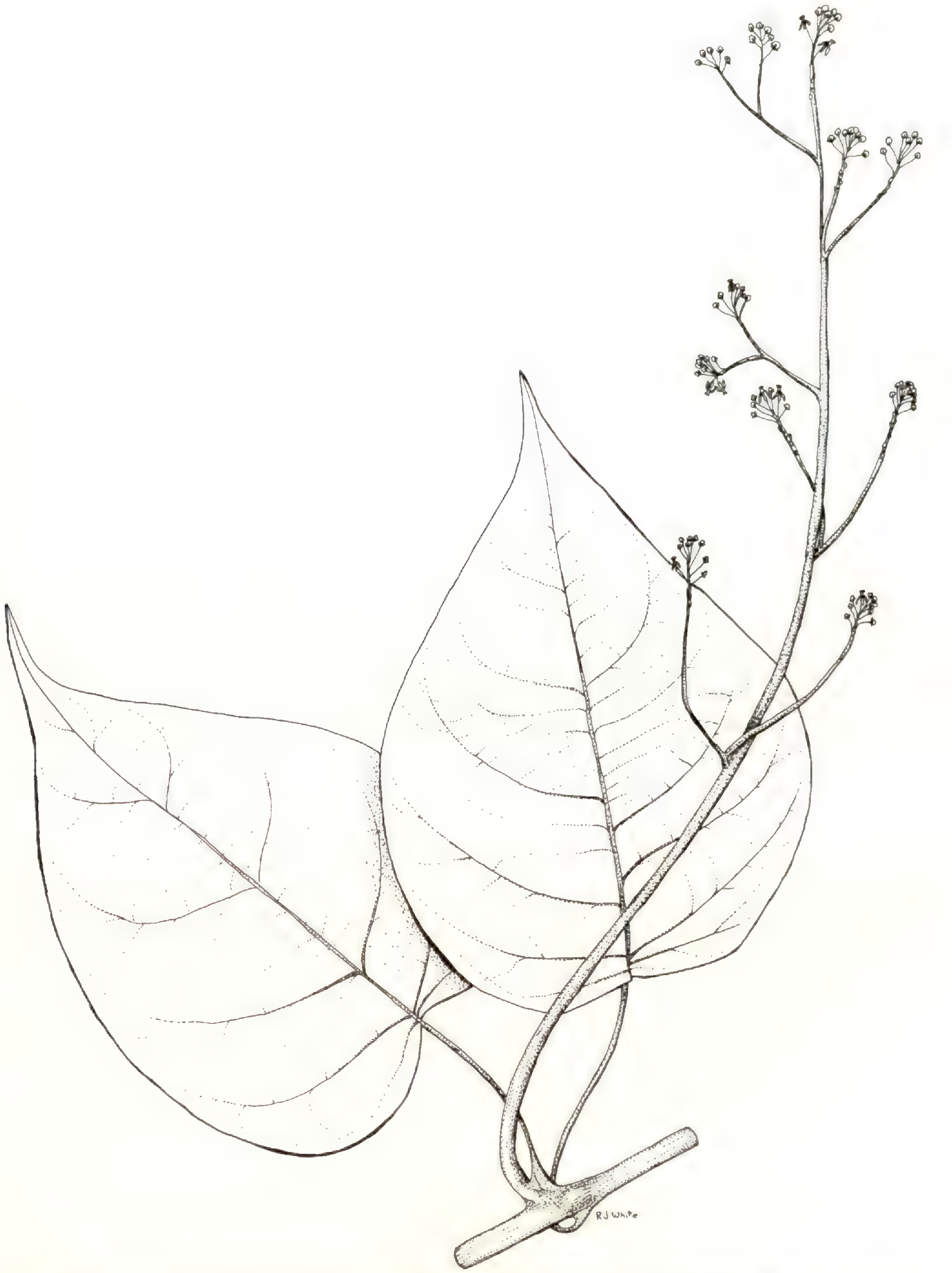


FIGURE 6. *Cynanchum cubense* (A. Rich.) Woodson, portion of stem with inflorescence (× ⅜). [After *Croat 11175* (MO).]

(Urb.) Woodson (Colombia, Venezuela, Ecuador, Peru) and *C. haughtii* Woodson (Ecuador), both of which have sepals longer than the petals.

CANAL ZONE: Barro Colorado Island, *Croat 11175, 12581* (both MO); *Hayden 125* (DUKE, MO). COCLÉ: El Cermeño, *Zetek 4528* (MO). PANAMÁ: Isla de Pedro Gonzales, *Dwyer 1697* (MO).

6. **Cynanchum magdalenicum** Dugand, Caldasia 9: 408. 1966. TYPE: Colombia, *Killip & Smith 14715* (MO, NY, US).

Slender herbaceous *vines*; stems glabrous or puberulent in the younger portion. *Leaves* glabrous but sparsely pubescent near the attachment of the petioles, ovate, basally cordate, apically acuminate, 1.6–2.5 cm long with a cluster of dactyliform glands at the base, 4.5–6 cm long and 2.8–3.8 cm wide; petioles glabrous. *Inflorescence* racemose, the rachis and pedicels fine puberulent; pedicels 7.1–7.6 mm long. *Flowers* with the calyx lobed to the base, the lobes 1.8–2.5 mm long and 1.4–1.6 mm wide, ovate, puberulent outside; corolla greenish-white, rotate, the lobes reflexed at anthesis, lanceolate, 6.4–6.9 mm long and 1.4–1.5 mm wide, glabrous inside and out; corona segments rhombic with a ± ligulate apical portion, nearly twice as long as the gynostegium, 3.8–3.9 mm long and 1.8–1.9 mm wide, the apices arching over the gynostegium; gynostegium short, broad, truncate-conical, 1.8–1.9 mm high. *Follicles* (from Colombian material) elongate-ovoid, smooth, glabrous, 5 cm long when immature and ca. 2 cm wide.

Known only from western Colombia and Panama, this lowland taxon is one of a group recognized by some workers as the genus *Roulinia*. The group is closely allied to *Metalepis*.

CANAL ZONE: Along the Trinidad River, *Pittier 3975* (US). PANAMÁ: Interamerican Highway just E of Bejuco, *Duke 4551* (MO).

6. BLEPHARODON

Blepharodon Dcne. *in* DC., Prod. 8: 603. 1844. TYPE: *B. lineare* (Dcne.) Dcne.

Vines, herbaceous or somewhat woody, sometimes erect. *Leaves* opposite, often subcoriaceous, glabrous. *Inflorescences* usually umbelliform or racemiform, few- or many-flowered, pedunculate from the leaf axils. *Flowers* usually greenish to whitish; calyx 5-lobed, with usually 5 glands inside at the base, generally short, ovate, obtuse; corolla valvate in bud, 5-lobed halfway or more to the base, the lobes ciliate or sometimes glabrous, campanulate; stamens affixed to the base of the corolla, the corona of 5 semi-vesicular sacs attached to the staminal tube, connate to the corolla or free from it, or of 5 membranous erect, cucullate, concave, or cymbiform segments with internal appendages, the filaments connate into a short tube, the anthers terminating in an inflexed membrane; pollinia pendulous, generally ovoid; stigma circular, apically depressed or shortly umbonate. *Fruits* a single follicle, smooth, mostly terete, apically acuminate; seeds comose.

With single outlying species in North America, the genus is centered in South America where 40–50 species are known.

FIGURE 7. *Blepharodon mucronatum* (Schlecht.) Dcne.—A. Flowering stem (× 3/5).—B. Flower (× 2 2/5).—C. Fruit (× 3/5). [After *Croat 6375* (MO).]

1. **Blepharodon mucronatum** (Schlecht.) Dcne. *in* DC., Prod. 8: 603. 1844.—FIG. 7.

Astephanus mucronata Schlecht., Linnaea 8: 518. 1833. TYPE: Mexico, *Schiede* (not seen).

Slender branched *vines*, glabrous throughout. *Leaves* subcoriaceous, lanceolate-oblong to elliptic, cuspidate-acuminate, basally rounded or obtuse, pale beneath with conspicuous, thin veins which close near the margins, 3–7 cm long and 1.5–3 cm wide; petioles 1–1.5 cm long. *Inflorescences* axillary, few-flowered;

peduncles slender, mostly 1–2 cm long; pedicels filiform, 1–2.5 cm long. *Flowers* with the calyx lobes oblong-ovate, obtuse, ca. 1.5 mm long and 0.5 mm wide; corolla greenish-white, campanulate, ca. 1 cm broad, the lobes lanceolate-oblong, obtuse, densely short pubescent inside, glabrous outside, ciliate along the margins, 5–6 mm long and ca. 3 mm wide; corona segments of 5 semi-vesicular sacs, free from the corolla, oval in outline, much shorter than the gynostegium, ca. 1.5 mm long and ca. 0.8 mm wide; gynostegium 2.5–3 mm high. *Follicles* smooth, glabrous, terete, fusiform with a long acuminate apex, 6–9 cm long, ca. 1.5 cm thick.

A vine of thickets or mixed forests, this species ranges from Mexico through Central America, Panama, and northern South America.

CANAL ZONE: Ancon Hill, *Duke 4582* (MO). Barro Colorado Island, *Croat 6375, 13159* (both MO). Pipeline Road, *Gentry 1898* (MO); *Croat 12366* (MO). 5–9 mi. N of Gamboa, *Gentry 1406* (MO). Chiva-Chiva Trail, Red Tank to Pueblo Nuevo, *Piper 5731* (US). Near France Field, *Blum & Dwyer 2118* (MO). Near beach at Ft. Kobbe, *Duke 4182* (MO). Las Cruces Trail, *Hunter & Allen 508* (MO). COCLÉ: Near El Valle de Antón, *Allen 1980* (MO, US). COLÓN: Summit of Cerro Santa Rita, *Allen 5108* (MO). Santa Rita Ridge lumber road, *Correa & Dressler 1067* (DUKE, MO). Santa Rita Ridge, East Ridge, *Dwyer & Correa 8399* (MO). Santa Rita Ridge, 4–5 mi. from Transisthmian Highway, *Gentry 6089* (MO). Santa Rita, *Gómez-Pompa & Gonzalez 3136* (MO). DARIÉN: Isla Saboga, *Duke 10371* (MO). PANAMÁ: Tocumen, *Dwyer 5545* (MO). Near beach at Nueva Gorgona, *Duke 4502* (MO). 5–6 mi. E of Chepo on Panamerican Highway, *Duke 4052* (MO). Tumba Muerto, *Stevens 848* (US). Cerro Campana, *Ebinger 918* (MO, US); *McDaniel 6842* (MO), *6906* (DUKE, FSU); *Duke 5973* (MO). Isla Espiritu Santo, *Duke 10451* (MO, OS). San José Island, *Erlanson 461* (US); *Harlow 27, 44* (both US); *Johnston 31, 194, 978* (all MO, US). Tobago Island, *Killip 3186* (US); *Macbride 2833* (US). VERAGUAS: Trail between Canazas and foot of Cordillera Central, headwaters of Río Canazas, *Allen 159* (MO).

7. SARCOSTEMMA[5]

Sarcostemma R. Br., Mem. Wern. Soc. 1: 50. 1809. TYPE: *S. viminale* (L.) R. Br.

Slender *vines*, herbaceous or suffrutescent, pubescent or glabrous, sometimes glaucous. *Leaves* opposite. *Inflorescence* axillary, umbellate, usually pedunculate. *Flowers* with the calyx small, 5-lobed, minutely 5-glandular within at the base, the lobes acute; corolla generally white, greenish-white, or sometimes purplish, broadly campanulate or subrotate, shallowly or deeply 5-lobate, usually depressed globose in bud; stamens inserted on the base of the corolla, the corona of 5 inflated vesicles adnate to the base of the staminal tube, usually equaling or overtopping the gynostegium, the apices flat, concave or convex, almost always joined by a fleshy annulus which is adnate to the corolla throat, its margin entire, filaments connate into a short tube, the anthers terminated by an inflexed membrane; pollinia pendulous, oblong or elongated; stigma flat or umbonate or with a short bifid apical beak. *Fruit* a single follicle usually slender, terete, acuminate, smooth, glabrous or pubescent.

Literature:

Holm, R. W. The American species of *Sarcostemma* R. Br. (Asclepiadaceae). Ann. Missouri Bot. Gard. 37: 477–560. 1950.

[5] For a list of synonyms see Holm (1950). Only these names have been used for Panamanian material.

A genus of about 35 species found throughout warm and tropical regions. The New World species are concentrated in South Amercia, the following three reported from Panama.

a. Leaf bases cordate ..... 1. *S. bilobum*
aa. Leaf bases attenuate to rounded, occasionally truncate but not cordate.
  b. Corolla rotate-subcampanulate, not constricted at the throat; ovaries white sericeous ..... 2. *S. clausum*
  bb. Corolla salverform, the tube constricted at the throat; ovaries glabrous ... 3. *S. glaucum*

1. **Sarcostemma bilobum** Hook. & Arn., Bot. Beechey's Voy. 438. 1841. TYPE: Beech. herb. (K, not seen).—FIG. 8.

S. lindenianum Dcne. *in* DC., Prod. 8: 541. 1844. TYPE: *Linden* (P, not seen).
Philibertia lindeniana (Dcne.) Hemsley, Biol. Centr.-Amer. Bot. 2: 318. 1881.
P. biloba (Hook. & Arn.) Gray, Proc. Amer. Acad. Arts 21: 395. 1886.
Funastrum lindenianum (Dcne.) Schltr., Fedde Repert. Sp. Nov. 13: 286. 1915.
F. bilobum (Hook. & Arn.) Macbr., Contr. Gray Herb. 49: 51. 1917.
Sarcostemma bilobum subsp. *lindenianum* (Dcne.) Holm, Ann. Missouri Bot. Gard. 37: 519. 1950.

Trailing or twining *vines*. *Leaves* oblong-ovate to suborbicular, shortly acuminate, deeply cordate, the sinus narrow and the lobes converging, pubescent or glabrate on both sides, 2–5 cm long and 1.5–4.0 cm wide; petioles 1.0–2.5 cm long. *Inflorescence* umbellate, to 35-flowered; peduncles 1.5–6 cm long; pedicels slender, to 3 cm long. *Flowers* with the calyx lobed to the base, the lobes linear to ovate, ca. 2.5 mm long, puberulent outside, glabrous within; corolla whitish, subrotate, the tube ca. 2 mm long, the lobes lanceolate, obtuse, reflexed, ciliate, puberulent inside, glabrous outside, 5–7 mm long and 3–3.5 mm wide; corona 5-vesicular, each vesicle pyramidal, widest below the middle, ca. 3 mm high, free from the annular ring; gynostegium ± cylindrical, shorter than the corona, ca. 2.5 mm high. *Follicles* to 8 cm long, 2 cm in diameter, puberulent, striate.

This is a primarily lowland species which ranges from Mexico to Colombia and Venezuela. The Panamanian material is similar to what Holm referred to as subsp. *lindenianum*, but cannot be regarded as distinct from the typical subspecies. Holm cited *Wedel 1755* as a putative hybrid between subsp. *bilobum* and subsp. *lindenianum*.

BOCAS DEL TORO: Water Valley, Chiriqui Lagoon, *Wedel 1755* (MO, US). DARIÉN: Patiño, *Duke 10530A* (OS). PANAMÁ: Above Chepo, Mamoni River, *Pittier 4729* (US). Vera Cruz, beach and sandy areas behind, *Lewis et al. 2996* (F, MO). Isla Tabaguilla, *Duke 5870* (MO).

2. **Sarcostemma clausum** (Jacq.) Roem. & Schult. *in* L., Syst. Veg., ed. 15. 6: 114. 1820.

Cynanchum clausum Jacq., Stirp. Amer. 1: 87, *t. 60*. 1763. TYPE: (not seen).
Funastrum clausum (Jacq.) Schltr., Fedde Repert. Sp. Nov. 13: 283. 1915.
F. seibertii Woodson, Ann. Missouri Bot. Gard. 24: 199. 1937. TYPE: Panama, *Seibert 637* (MO, holotype).

Herbaceous *vines* often forming dense tangles over shrubs, pale-colored, usually glaucescent; stems glabrous or nearly so. *Leaves* nearly linear to oblong,

FIGURE 8. *Sarcostemma bilobum* Hook. & Arn.—A. Flowering stem (× 3/5).—B. Flower (× 6). [After *Duke 5870* (MO).]

somewhat thickened and fleshy, acuminate to cuspidate, usually obtuse or rounded at the base, glabrous or sometimes pubescent beneath, 3–7 cm long and mostly 8–15 mm wide; petioles 2–9 mm long. *Umbels* few- to many-flowered; peduncles 3–10 cm long; pedicels short pilose, 1.2–2 cm long. *Flowers* with the calyx densely short pilose, 5-lobed, the lobes lanceolate, acute, ca. 3 mm long and 1.5 mm wide; corolla rotate-subcampanulate, 1.0–1.4 cm broad, the tube lobed nearly to the base, greenish-white, densely short-pilose outside, glabrous inside, the lobes 6–7 mm long and 3–4 mm wide, broadly ovate, rounded, or

obtuse and apiculate; corona vesicles ovoid, attached basally to the fleshy annular ring, ca. 2.5–3.0 mm high; gynostegium shorter than the corona; stigma umbonate, ovaries densely white sericeous. *Follicles* 5.0–6.5 cm long and ca. 1 cm wide, pubescent or glabrate, smooth.

This is a commonly encountered species of the lowlands of Mexico and Central America, South America and the West Indies.

BOCAS DEL TORO: Banks of Changuinola River, *Dunlap 289* (F, US). Ca. ½ mi. from Changuinola River entry into Atlantic, *Lazor & Tyson 2685* (FSU). Changuinola to 5 mi. S at junction of Río Changuinola and Río Terebé, *Lewis et al. 932* (MO, US). CANAL ZONE: Culebra Cut and vicinity, *Hunter & Allen 775* (MO). Barro Colorado Island, *Bangham 413* (F, US); *Croat 4959* (MO), *6172* (DUKE, MO), *6870, 8169, 8295, 11928, 13234* (all MO); *Ebinger 577* (MO); *Foster 941* (DUKE); *Kenoyer 501* (US); *Shattuck 315* (F, MO), *1114* (MO); *Starry 48* (F); *Wetmore & Abbe 132* (F); *Wilson 66* (F, MO); *Woodworth & Vestal 390* (F, MO), *537* (F). COCLÉ: El Valle de Antón, bog, *Dwyer 1828* (MO). 1–5 mi. S of Antón on old road to coast, *Tyson & Blum 2569* (SU, MO). HERRERA: Cienaga Juncalillo, near Correa, *McDaniel 8027* (DUKE, FSU). PANAMÁ: Between Goofy Lake on Cerro Azul and main highway, *Correa & Dressler 433* (DUKE, FSU, MO). Between El Jagua Hunting Club on Río Jagua and El Congor Hill, *Hunter & Allen 482* (MO, US). Near Arenoso, lower Río Trinidad, *Seibert 637* (MO).

3. **Sarcostemma glaucum** H.B.K., Nov. Gen. Sp. Pl. 3: 194. 1819. TYPE: *Humboldt & Bonpland* (P, not seen).

Funastrum glaucum (H.B.K.) Schltr., Fedde Repert. Sp. Nov. 13: 285. 1915.

Glabrous, herbaceous *vines*. *Leaves* elliptic or narrowly elliptic, occasionally oblong or ovate, somewhat fleshy, glaucous; petioles 3–8 mm long, the blades 5–9 cm long and 0.5–3.8 cm broad. *Inflorescences* umbellate, 10–40-flowered; peduncles 5–12 cm long; pedicels thin, mostly ca. 2 cm long. *Flowers* with the calyx deeply lobed, the lobes 1.0–1.5 mm long and 0.5–0.8 mm wide, ovate, the margins ciliate, otherwise glabrous; corolla white or greenish-white, short salverform, the tube ca. 2 mm long, slightly but noticeably constricted at the orifice, the lobes ovate, obtuse, the margins ciliate, puberulent inside, glabrous outside, 4–6 mm long and ca. 2.5 mm wide; the fleshy annular ring prominent, adnate to the corolla and bases of the corona vesicles, the vesicles ovoid, pointed, 1.5–2.0 mm long; gynostegium ca. 2 mm high; ovaries glabrous. *Follicles* to 10 cm long, 1 cm in diameter, glabrous.

This species occurs in the lowlands of Panama, Colombia, Venezuela and Peru.

COCLÉ: Aqua Dulce, *Pittier 4977* (F, US). DARIÉN: Patiño, *Duke 10530* (MO). HERRERA: Near Chitré, *Allen 1090* (MO). LOS SANTOS: Beach at Monagre, *Burch et al. 1208* (MO). 3 mi. S of Carreta, *Burch et al. 1253* (MO, US). Ca. 7 mi. S of Chitré, *D'Arcy & Croat 4170A*. Río Tonosí, near Tonosí, *Lewis et al. 1585A* (MO), *1586* (F, MO). Monagre Beach, *Tyson et al. 2895* (MO). PANAMÁ: Juan Díaz, *Standley 30510* (F, US).

8. MARSDENIA

Marsdenia R. Br., Mem. Wern. Soc. 1: 28. 1811. TYPE: *M. tinctoria* R. Br.

Herbaceous or woody *vines*, rarely erect, pubescent or glabrous. *Leaves* opposite. *Inflorescences* umbelliform or paniculate, terminal or axillary. *Flowers*

generally small, tubular; calyx 5-lobed, 5- to several-glandular within at the base or eglandular, the lobes acute or obtuse; corolla campanulate to urceolate or occasionally subrotate, 5-lobed, the throat usually closed or nearly so by dense pubescence or an annulus, rarely glabrous within, the lobes obtuse; stamens inserted near the base of the corolla, the corona 5-parted, the segments adnate to the staminal column and frequently to the dorsal side of the anthers, usually free from the corolla, erect, apically free, flattened, fleshy or membranaceous, the filaments connate into a short tube, the anthers with a thin inflexed apical membrane; pollinia strictly erect, generally ovoid or narrowly oblong; stigma usually apically convex or rostrate, occasionally flat or depressed. *Fruit* usually single follicles, thick, ± ellipsoidal in outline, smooth or occasionally longitudinally winged, pericarp often hard and woody when dry; seeds comose.

There are about 50 species of *Marsdenia* in the tropics and subtropics of the New World and possibly an equal number indigenous to the Old World. About 25 species are found in Mexico and Central America.

Literature:

Rothe, W. Über die Gattung *Marsdenia* R. Br. und die Stammpflange der Condurangorinde. Bot. Jahrb. (Syst.) 52: 354–434. 1915.

a. Flowers pinkish, striped with purple; corolla lobes linear ..... 1. *M. trivirgulata*
aa. Flowers green, yellow, or red; corolla lobes elliptic, ovate, or deltoid.
  b. Leaves densely white villous beneath; flowers green ..... 4. *M. panamensis*
  bb. Leaves glabrous to glabrate beneath, not villous; flowers red, yellow, or green.
    c. Flowers greenish to yellowish; inflorescence usually with less than 10 flowers.
      d. Pedicels filiform, more than 1 cm long; stems with dense warty excrescences; highland species ..... 7. *M. rotheana*
      dd. Pedicels stouter, less than 5 mm long; stems smooth; lowland species ..... 6. *M. crassipes*
    cc. Flowers red or red brown; inflorescence usually with 8 or more flowers.
      e. Corolla tube constricted at the throat, the lobes conspicuously short pilose; leaves mostly less than 10 cm long ..... 2. *M. margaritaria*
      ee. Corolla tube not constricted, lobes glabrous on the surface; leaves mostly more than 10 cm long.
        f. Inflorescence many-flowered; calyx lobes ovate; leaf bases cordate ..... 3. *M. maculata*
        ff. Inflorescence with 8–12 flowers; calyx lobes orbicular or nearly so; leaf bases rounded ..... 5. *M. dressleri*

1. **Marsdenia trivirgulata** Bartlett, Proc. Amer. Acad. Arts 44: 632. 1909. TYPE: Guerrero, Mexico, *Pringle 10333* (MO).

Slender, ± woody *vines*. *Stems* nearly glabrous or in younger portions with 2 lines of puberulence. *Leaves* membranaceous, narrowly elliptic to ovate-elliptic, 2.5–7.5 cm long and 1.5–2 cm wide, apically acuminate, basally acute or attenuate, densely to sparsely pubescent on both sides; petioles slender, 7–8 mm long. *Inflorescences* few-flowered, sparsely puberulent; peduncles ca. 1 mm long; pedicels 4–5 mm long. *Flowers* with the calyx 5-lobate, the lobes ovate, obtuse, white ciliate, sparsely puberulent outside, glabrous inside, ca. 1.5–2 mm long and 1–1.5 mm wide; corolla pale pinkish with purple stripes or blotches, campanulate, glabrous outside, the lobes finely puberulent inside, linear-oblong,

several times as long as the tube, ca. 6 mm long and 2 mm wide, obtuse, a low fleshy appendage tipped with hair inserted on the tube between the lobes; corona of 5 fleshy, ± rectangular segments, each segment attached at its middle to the dorsal part of the stamen; anthers with a tridentate lobed, inflexed membrane, the middle tooth long acuminate; stigma head rostrate, with a conical apically bifid beak ca. 1 mm long. *Fruit* unknown.

The linear or ligulate corolla lobes with their purplish markings make this one of the more easily recognized members of the family in Panama. It ranges from southern Mexico through Honduras, Costa Rica, and Panama.

CANAL ZONE: Farfan Beach, from Thatcher Highway to Palo Seco, *Lewis et al. 48* (DUKE, F, MO). HERRERA: Near Chitré, *Allen 1092* (F, MO).

2. **Marsdenia margaritaria** Foster *in* Johnston, Sargentia 8: 249. 1949. TYPE: Panama, *Johnston 1190* (MO).

Woody *vines*. *Stems* glabrous when young, becoming corky and somewhat plated with age. *Leaves* lanceolate to oblong-ovate, acute or acuminate, basally cuneate to rounded, mostly glabrous, the margins revolute, 9–12 cm long and 3–4.5 cm wide; petioles 1.5–2 cm long. *Inflorescences* umbelliform, few- to several-flowered; peduncles 2–5 mm long; pedicels 2–3 mm long. *Flowers* greenish to brown; calyx lobes ovate, puberulent outside, glabrous inside, the margins ciliate, apically obtuse, ca. 2 mm long and 1.5 mm wide; corolla urceolate, the tube 3–5 mm long, glabrous outside, inside with dense retrorse hairs opposite the anthers, the lobes ciliate, short pilose on the surface except for the region of overlap of adjacent lobes, ovate, obtuse, reflexed, ca. 2.5 mm long and nearly as wide; gynostegium ca. 2.5 mm high; corona lobes fleshy, broadly ovate, ca. 1–1.5 mm high, equally wide. *Fruit* not known.

This species is known only from Panama where it seems to be restricted to drier habitats. Pittier reports "cuingara" or "cuinbara" as common names.

COCLÉ: Aguadulce, *Pittier 4904* (US). Near Penonomé, *R. S. Williams 430* (NY). PANAMÁ: San José Island, *Johnston 759, 850, 1190* (all MO).

3. **Marsdenia maculata** Hook. f., Bot. Mag. *t. 4299*. 1847. TYPE: (not seen).

Large coarse *vines* with thick woody stems. *Leaves* oblong-elliptic to ovate to suborbicular, apically short acuminate, basally truncate to shallowly cordate, glabrous, 10–25 cm long and 5–20 cm wide; petiole 1.5–5 cm long. *Inflorescence* umbelliform, occasionally short-branched and more open, many-flowered, glabrous or puberulent; peduncles ca. 1 cm long; pedicels mostly 0.8–1 cm long. *Flowers* red or reddish-brown; calyx lobes ovate, 3–4 mm long and 2–3 mm wide, glabrous except for the ciliate margins; corolla suburceolate, lobed to about the middle, the tube 3–4 mm long, the lobes oblong-ovate, apically broadly rounded, glabrous except for the ciliate margins of the lobes and the tufts of retrorse hairs opposite the lobes on the inside of the tube; corona of linear-oblong, obtuse, fleshy segments, noticeably shorter than the gynostegium; stigma terminated by

FIGURE 9. *Marsdenia panamensis* Spellman.—A. Flowering stem (× ½).—B. Gynostegium and corona (× 5). [After *Croat* 9752 (MO).]

a conical, undivided beak. *Follicles* ellipsoidal, smooth, glabrous, to 22 cm long and 5 cm in diameter.

As here delimited, the species occurs from Guatemala through Panama and into Colombia and Venezuela. It is also found in the Lesser Antilles.

Treated by Rothe (1915) as a synonym of *M. macrophylla* (H. & B.) Fourn., the taxon was considered by Williams in the *Flora of Guatemala* to be distinct. While preliminary observation suggests concurrence with Williams, his key characters weaken as one looks at the South American and Panamanian material.

Only an intensive study of the 4 or 5 taxa related to *M. maculata* will shed light on the problem.

BOCAS DEL TORO: Isla Colón, Chiriquí Lagoon, *Wedel 1055* (MO, US). Near Chiriquí Lagoon, *Wedel 1184* (MO, US). CANAL ZONE: Near Summit, *Allen 4516* (F, MO, US). Road K-10, 1–2 mi. from Kobbe-Arrayan Highway, *Duke 11708* (MO). DARIÉN: Isla Saboga, *Duke 10355* (MO). LOS SANTOS: Between Los Santos and Guararé, *Woodson et al. 1197* (MO). PANAMÁ: San José Island, Perlas Archipelago, *Erlanson 503* (US); *Johnston 876* (MO). Pacheca Island, Perlas Islands, *Tyson 5609* (FSU, MO).

4. **Marsdenia panamensis** Spellman, sp. nov.[6] TYPE: Panama, *Croat 9752* (MO, holotype; F, NY, isotypes).—FIG. 9.

Coarse *vines*. *Stems* glabrous when mature, juvenile stems puberulent in lines. *Leaves* ovate, apically rounded and abruptly short acuminate, basally cordate, glabrous above, densely white villous beneath, 11–17 cm long and 10–13 cm wide; petioles 2.5–4 cm long. *Inflorescences* umbelliform, many-flowered, densely short villous throughout; peduncles 1–2 cm long; pedicels 4–6 mm long. *Flowers* greenish; calyx lobes ovate, densely villous outside, glabrous inside, 3–4 mm long and 2–3 mm wide; corolla campanulate, glabrous throughout except for patches of retrorse hairs inside the tube, lobes somewhat fleshy, lanceolate-obtuse, ca. 5 mm long and 2 mm wide, the margins thin and papery with inconspicuous cilia; corona of separate, carnose, deltoid segments; gynostegium 4–5 mm high; stigma head with a conical bifurcate apical appendage. *Fruit* unknown.

Known only from the type collection.

LOS SANTOS: Punta Mala, *Croat 9752* (F, MO, NY).

5. **Marsdenia dressleri** Spellman, sp. nov.[7] TYPE: Panama, *Dressler 3451* (MO, holotype).—FIG. 10.

Glabrous *vines*. *Leaves* elliptic to occasionally ovate, dark green and subnitid above, lighter beneath, apically short acuminate, basally rounded, 10–12 cm long and 4.5–6 cm wide, the midvein thickly prominent, with 3 pairs of more prominent lateral veins which merge to form an irregular marginal vein; petioles 1–1.5 cm long. *Inflorescences* umbelliform, ca. 10-flowered, glabrous; peduncles ca. 3 mm long; pedicels 2–3 mm long. *Flowers* red-brown, ca. 7–8 mm long; calyx lobes imbricate when expanded, thickened, suborbicular, glabrous except for the ciliate margins, 2.5 mm long, equally wide; corolla tube cylindrical 5–6 mm long, glabrous outside, retrorsely pubescent in clusters of hairs inside, weakly strigose at the mouth, the lobes elliptic, 3–4 mm long and 2–3 mm wide, glabrous,

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[6] *Marsdenia panamensis* Spellman, sp. nov. Folia ovata basaliter cordata, supra glabra subter dense villosa; inflorescentia umbelliformis omnino densa villosa, floribus multis; calyx lobis ovatis extus dense villosis; corolla campanulata glabra olivacea, lobis carnosis, lanceolato-obtusis; corona carnosa, segmentis deltoideis; stigmate rostrato, rostro conico, apice bifurcato.

[7] *Marsdenia dressleri* Spellman, sp. nov. Plantae scandentes omnino glabrae; folia elliptica vel ovata, lamina discolore, supra subnitida; inflorescentiae umbelliformes ca. 10 floribus ornatae; calyx lobis suborbicularibus; corolla angusto-infundibuliformis, lobis subellipticis, glabris, ciliatis, rubiginosis; corona carnosa, segmentis lanceolatis, convexis; stigma rostratum, rostro crasso conico, minute papilloso, apice integro.

FIGURE 10. *Marsdenia dressleri* Spellman.—A. Flowering stem (× 3/5).—B. Gynostegium and portion of corona (× 6). [After *Dressler 3451* (MO).]

the margins ciliate; corona 5-segmented, segments carnose, convex, lanceolate, closely appressed to the stamens; gynostegium ca. 4 mm high; stigma head topped by a thick, conical rostrum which is undivided and minutely papillose. *Follicles* unknown.

Known only from the type collection.

PANAMÁ: La Eneida, region of Cerro Jefe, *Dressler 3451* (MO).

6. **Marsdenia crassipes** Hemsl., Biol. Cent. Amer. Bot. 2: 337. 1882. TYPE: Panama, Colón, *Hayes 373* (K, not seen).

Slender glabrous *vines*. *Leaves* ovate to oblong-elliptic, apices acute to acuminate, bases rounded to somewhat cuneate, 8–15 cm long and 5–7 cm wide; petioles stout, 1–1.5 cm long. *Inflorescences* umbelliform, glabrous, few-flowered; peduncles and pedicels ca. 1–2 mm long. *Flowers* greenish-yellow; calyx lobes broadly ovate, 2–2.3 mm long, equally wide, glabrous, the margins ciliate; corolla campanulate, glabrous, the tube ca. 2 mm long, the lobes spreading, narrowly ovate, ca. 2–3 mm long and 2 mm wide, glabrous, the margins white, ciliate; corona segments carnose, elongate, ca. 2.5 mm long; gynostegium 2–2.5 mm high, slightly exserted, terminated by a short conical beak. *Follicles* unknown.

This species is known only from lowland Panama.

CANAL ZONE: Barro Colorado Island, *Shattuck 341* (F). PANAMÁ: Near Arraíjan, *Woodson et al. 779* (MO). SAN BLAS: Isla Soskatupo, *Duke 8936* (MO, OS).

7. **Marsdenia rotheana** Woodson, Ann. Missouri Bot. Gard. 37: 408. 1950. TYPE: Panama, *Allen 4495* (MO, holotype).

Vines. *Stems* with warty-appearing bark. *Leaves* thick, glabrous except on the veins beneath, oblong-elliptic to ovate, acuminate, basally truncate to slightly rounded, 6–10 cm long and 3–4 cm wide; petiole sparsely pubescent, 0.5–1 cm long. *Inflorescences* umbelliform, 1- or few-flowered; peduncle 3–5 mm long; pedicels 12–15 mm long or more. *Flowers* yellow; calyx lobes ovate, ca. 2 mm long and 1.5 mm wide, glabrous, margins ciliate; corolla campanulate, glabrous, the tube ca. 2.5 mm long, the lobes oblong-ovate, obtuse, ciliolate, 3–4 mm long and ca. 2 mm wide; corona lobes subquadrate, apiculate, ca. 2 mm long. *Fruit* (described from Colombian material) borne singly, terete or nearly so, fusiform, apically long acuminate, 11–22 cm long, ca. 7.5–9.5 mm in diameter, smooth, glabrous.

Known only from the type and one collection recently made by Gentry and Forrero from Choco, Colombia. The latter collection is the only fruiting collection.

COCLÉ: Cerro Pajita, region N of El Valle de Antón, *Allen 4495* (MO).

9. STEPHANOTIS

Stephanotis Thouars, Nov. Gen. Madag., 11. 1808. LECTOTYPE: S. *thouarsii* Brongn.

Woody *vines* with thickened leaves. *Inflorescences* umbellate. *Flowers* large, fragrant, white or yellow; calyx lobes usually ovate; corolla tubular, the tube usually inflated at the base, fleshy, the lobes contorted in bud, rounded-elliptic when expanded; stamens coherent into a column arising from the base of the corolla tube, the corona 5-parted, segments carnose, joined individually to the dorsal sides of the stamens; pollinia small, erect; stigma head usually with a conical appendage, exserted or included. *Fruit* generally a single follicle, thick, blunt or acuminate; seeds comose.

A small genus of 5–15 species native to Madagascar, Africa, and Malaysia. Apparently only S. *floribunda* has found its way into common use as an ornamental.

1. **Stephanotis floribunda** Brongn., Ann. Sci. Nat. Bot., sér. 2. 7:30. 1837. TYPE: Not seen.

Glabrous *vines*. *Leaves* elliptic, coriaceous, shining, apically mucronulate, basally rounded, 7–10 cm long and 4.5–6 cm wide; petioles 1.5–2 cm long. *Inflorescences* umbellate, 5–8-flowered; peduncles ca. 1 cm long; pedicels 2–2.5 cm long. *Flowers* white, sweetly fragrant; calyx lobes ovate, 5–6 mm long and 3–4 mm wide; corolla salverform, the tube 2.2–2.7 cm long, the lobes ovate, 1.1–1.2 cm long and 6–8 mm wide; corona lobes ovate, fleshy, shorter than the anthers; gynostegium much shorter than the corolla tube; stigma head conical, undivided. *Follicle* ellipsoid, 7–10 cm long, glabrous, fleshy.[8]

Commonly cultivated species in tropical areas, especially the Caribbean, it is known in temperate regions as a house plant. Although known from only one collection from Panama, the species undoubtedly enjoys some popularity as a garden plant.

PROVINCE UNKNOWN: Aria's Place, *Standwood 485* (MO).

10. HOYA

Hoya R. Br., Mem. Wern. Soc. 1: 26. 1811. TYPE: *H. carnosa* (L.) R. Br.

Mostly epiphytic *vines*; stems glabrous, subligneous. *Leaves* thick and fleshy on usually stout petioles. *Inflorescences* racemose but appearing umbelliform, the rachis gradually lengthening with the flowering season. *Flowers* pedicellate, showy, pink, white, purple, or rarely yellow; calyx lobes small, inconspicuous, usually glabrous; corolla rotate, fleshy and often waxy-appearing, the lobes flat, convex, or sometimes reflexed, glabrous or pubescent; corona segments prominent, the lower segments appearing star-like or ascending along the staminal column and fleshy, the upper lobes usually in the form of an erect tooth resting against the anther, staminal column short, connivent over the stigma head; pollinia erect. *Fruit* a single or pair of follicles, slender or thickened, fusiform to oblong; seeds comose.

A genus of perhaps 80–100 mostly Asian species, no more than 3 or 4 species, of which the following is by far the most popular, are commonly encountered in cultivation.

1. **Hoya carnosa** (L.) R. Br., Mem. Wern. Soc. 1: 26. 1811.

Asclepias carnosa L., Suppl. 170. 1781. TYPE: (not seen).

Coarse glabrous *vines*. *Leaves* thick, coriaceous, shining, ovate to ovate-elliptic, acuminate, basally rounded, 5–8 cm long and 3–4 cm wide; petioles 1–

[8] Fruit description based on that found in Bailey's *Standard Cyclopedia of Horticulture.*

1.5 cm long. *Inflorescences* indeterminate umbelliform racemes; peduncles ca. 1 cm long; pedicels 2–3 cm long. *Flowers* cream-pinkish, waxy-appearing, ca. 1.5 cm in diameter; calyx lobes elliptic, ca. 3 mm long and 1 mm wide; corolla rotate, lobes triangular, 4 mm long and 4 mm wide at the base; corona segments forming a star-shaped structure, the points alternating with the corolla lobes, the segments ca. 3 mm long and 2 mm wide. *Follicles* smooth, acuminate.[9]

In addition to *H. carnosa*, two other species of *Hoya* may be encountered as ornamentals, *H. obovata* Dene., which is characterized by white flowers and heart-shaped leaves, and *H. purpureo-fusca* Hook., which has pinkish to purple flowers with densely hairy corollas. As a group, the genus *Hoya* is commonly known as "wax-vine."

CANAL ZONE: Hospital grounds at Ancón, *Mason s.n.* (US).

11. FISCHERIA

Fischeria DC., Cat. Hort. Monsp. 112. 1813. TYPE: *F. scandens* DC.

Herbaceous or suffruticose, lactiferous *vines*; stems terete, pubescent, the hairs of 2 types, short brown puberulent hairs overtopped by brown, septate, pilose hairs to 5 mm long of variable density but rarely lacking. *Leaves* petiolate, membranaceous to coriaceous, sparsely to densely pubescent on both surfaces, especially along the major veins, usually basally cordate, the sinuses narrow, the lobes frequently imbricate, usually with a cluster of digitiform glands at the juncture of the petiole and blade. *Inflorescences* interaxillary, at first umbelliform, becoming racemose, brown puberulent throughout with short hairs usually overtopped by longer ones. *Flowers* pedicellate; calyx deeply 5-lobed, abaxially puberulent or puberulent and pilose, adaxially glabrous or pubescent, 1 or 2 digitiform glands present in each sinus, lobes ovate to lanceolate or subulate; corolla subrotate, greenish, yellowish, or white, the tube short, usually not exceeding 2 mm, lobes ovate to suborbicular, canaliculate or plane, abaxially short-strigose to glabrate, glabrous along those parts of the margins which are imbricate in bud, adaxially pubescent, the hairs usually flattened, septate, and whitish, the surfaces frequently papillate beneath the pubescence; stamens connate to the top of the corona, above the corona merely connivent, corona carnose, lobed, angular, or entire, longitudinally striate-sulcate, fimbriate, rarely smooth, basally adnate to the corolla and for its full length to the staminal filaments, apically abutting the underside of the peltate stigma head and held in position by the inflexed terminal membranes which wholly or partially cover the top of the stigma head; stigma head broadly 5-angled, plane or slightly depressed in the center, the styles short, the ovaries obliquely ovoid to ellipsoid, glabrous to densely pubescent, only one developing in fruit; pollinia inserted horizontally or nearly so, subreniform, the fertile portion ± lunate, the dorsal margins pellucid, sterile. *Follicles* obliquely ovoid to ellipsoid, glabrous or minutely pubescent, smooth or striate; seeds compressed ovoid, the marginal wings coarsely and irregularly toothed in the lower half.

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[9] Fruit description taken from Bailey's *Standard Cyclopedia of Horticulture.*

FIGURE 11. *Fischeria funebris* (Donn.-Sm.) Blake.—A. Flowering stem (× 1/7).—B. Flower (× 2⅖). [After *Erlanson 267* (MO).]

A genus of about 12 recognized taxa which range from southern Brazil throughout most of South America through the lowlands of Panama and along the Atlantic slopes of Central America to Mexico and the West Indies.

a. Sepals shorter than the petals; petals strongly crispate apically on both margins ..... 2. *F. columbiana*
aa. Sepals much longer than the petals; petals strongly crispate on only one margin or not at all strongly crispate.
  b. Petals broadly ovate to suborbicular, conspicuously long ciliate on one or both margins; corona entire ..... 1. *F. funebris*
  bb. Petals ovate or lanceolate-ovate, eciliate; corona 5-lobate ..... 3. *F. panamensis*

1. **Fischeria funebris** (Donn. Sm.) Blake, in Jour. Washington Acad. Sci. 14: 293. 1924.—FIG. 11.

F. martiana var. *funebris* Donn. Sm., Bot. Gaz. (Crawfordsville) 24: 398. 1897. TYPE: Costa Rica, *Tonduz 9936* (US).
F. blepharopetala Blake, Contr. U. S. Natl. Herb. 20: 244. 1919. TYPE: Colombia, *Curran 206* (US).

Herbaceous *vines*. *Leaves* elliptic or occasionally narrowly ovate, apically acute to acuminate, basally shallowly cordate, the sinus rarely 1 cm deep, the lobes sometimes imbricate when younger, mostly 10–14 cm long, occasionally longer on older stems, 4.5–8.5 cm wide, scabrous above except on the midrib which

is conspicuously hirsute with brown, septate hairs, velutinous to tomentose beneath; petioles mostly 1–3.5 cm long, puberulent and sparsely to densely pilose with hairs 2–3 mm long. *Inflorescences* puberulent and pilose throughout; peduncles commonly 4–10 cm long, occasionally to 22 cm when older; pedicels (1.5–)2–3(–4.5) cm long. *Flowers* white or white tinged with pink; calyx abaxially brown puberulent and pilose, adaxially glabrous or nearly so, the lobes lanceolate to lanceolate-subulate, usually greatly exceeding the corolla lobes, (7–)9–13(–17) mm long and 1.6–2.4 mm wide; corolla 1.5–2.0 cm in diameter, the lobes broadly ovate to suborbicular, 5.5–7.7(–8.6) mm long and (4.5–)5–6 (–7.5) mm wide, adaxially glabrate to densely pubescent with long, white, septate hairs usually arrayed in a triangular pattern, crispate near the apex on one margin, one or both margins ciliate, but the crisped margin always with long, white, septate, dense cilia to 2 mm long; corona usually entire or sometimes remotely 5-angular, the margins striate-sulcate, column smooth, 1.5–2 mm high; gynostegium 2.5–3 mm high, the inflated portion of the stamens suborbicular in surface outline, the staminal membranes usually triangular and covering most of the stigma head; ovaries usually sparsely pubescent, occasionally glabrous. *Follicles* unknown.

This species grows in wet forests and edges from near sea level to about 500 m and ranges from Costa Rica through Panama and into northern Colombia. It is a distinctive species with its long-ciliate corolla lobes.

CANAL ZONE: Barro Colorado Island, *Aviles s.n.* (F); *Bailey & Bailey 286* (B, F); *Shattuck 816* (F, MO). Pipeline Road, 5 mi. N of Gamboa, *Gentry 4863* (MO). Near Gatun Station, *Hayes 388* (NY). W of Limon Bay, Río Pina-Río Media divide, *Johnston 1809* (A, MO). Pipeline Road, 0–11.1 mi., *Lewis et al. 5413* (DUKE, MO). Navy Reservation N of Gamboa, *Robyns 65–47* (G, MO). 12 mi. S of Colón on Río Providencia, *Tyson & Blum 3939* (FSU). COLÓN: Near Puerto Pilón on road between Climatological Station at Agua Clara and Puerto Pilón, *Correa & Dressler 1190* (MO). Trail along first river W of Portobelo, *Gentry 5144* (MO). DARIÉN: Above Paca, *Williams 750* (NY, US). PANAMÁ: San José Island, *Erlanson 184* (G, U, US), *238* (G, P, US), *267* (G, NY, US); *Johnston 554* (BM, G, US). SAN BLAS: Permé *Cooper 282* (F, G, NY, US). Headwaters of Río Mulatupo, *Elias 1760* (MO).

2. **Fischeria columbiana** Schltr., Bot. Jahrb. (Syst.) 37: 623. 1906. TYPE: Colombia, *Lehmann 9066* (F, K).

Leaves ovate to elliptic, apically acuminate to short caudate, basally shallowly cordate, frequently imbricate-lobed, mostly 11–14 cm long and 5–8 cm wide, the narrowed apices ca. 1 cm long, scabrous above, scabrous to strigose beneath, densely so along the veins; petioles 4–5 cm long, puberulent and sparsely pilose. *Inflorescences* densely brown puberulent throughout with sparse overtopping pilose hairs; peduncles mostly 12–15 cm long; pedicels usually 2.5–3.3 cm long, rarely with pilose hairs. *Flowers* 1.8–2 cm in diameter; calyx abaxially brown puberulent, occasionally with one to a few longer pilose hairs, adaxially glabrous or nearly so, the lobes ovate to lanceolate-ovate, obtuse, 4–5 mm long and 2–3 mm wide; corolla greenish-white, the lobes ovate, obtuse, 7.5–8.5 mm long and 4–5 mm wide, adaxially papillate in a prominent median band to 1 mm or more wide, densely to sparsely hirsute along the margin of the band of papil-

lae with non- or uni-septate, flattened, and pointed hairs to ca. 0.4 mm long, ciliate along one margin, the cilia multiseptate, ca. 0.5 mm long, strongly crispate near the apex on both margins, undulate below the crisped portions; corona 5-lobate, the surface vermiform-fimbriate, ca. 1 mm high; gynostegium ca. 2 mm high, inflated portions of the stamens thin, subquadrate in surface outline, staminal membranes broadly rounded, covering most of the stigma head; ovaries glabrate. *Follicles* unknown.

This species occurs in moist to wet thickets and woodland edges along streams from southwestern Panama to Ecuador from near sea level to ca. 1500 meters.

A remarkably constant species throughout its range, *F. columbiana* is most closely related to *F. polytricha* Dcne. of northern Mato Grosso, Brazil.

DARIÉN: Tres Bocas on the Río Cuasi, *Kirkbride & Duke 1366* (MO).

3. **Fischeria panamensis** Spellman, sp. nov.[10] TYPE: Panama, *Allen 1644* (MO, holotype; F, GH, NY, US, isotypes).

Leaves elliptic to ovate, rarely obovate, apically acuminate, the acumina sometimes prolonged into short caudicles, basally shallowly cordate, the sinuses rarely more than 1 cm deep, the lobes sometimes imbricate, blades mostly 9–15 cm long, to 20 cm or more when older, 4–8(–12) cm wide, above scabrous or rarely short pilose, beneath softly tomentose to velutinous; petioles usually 2–4 cm long, puberulent and pilose. *Inflorescences* sparsely to densely long pilose throughout; peduncles mostly 5–10 cm long, occasionally elongating with age to 16 cm or more; pedicels commonly 2.5–3.5 cm long. *Flowers* yellowish or whitish green; calyx abaxially brown puberulent with short hairs and sparse or dense pilose hairs to ca. 3 mm long, the lobes lanceolate-acuminate, usually 5 or more times longer than broad, (9–)11–15(–20) mm long and 2–2.5(–3.5) mm wide, the margins conspicuously undulate; corolla 17–21 mm in diameter, lobes ovate-acute, 6.5–8.5 mm long and 4.5–6.5 mm wide, adaxial surface with a median band of inconspicuous papillae overtopped by a triangular pattern of sparse to dense flattened hairs, the margins glabrate, crispate apically on one or occasionally both margins; corona 1–1.5 mm high, longitudinally striate-sulcate, distinctly 5-lobate; gynostegium 2–3 mm high, the inflated portions of the stamens elliptic to suborbicular in outline, the staminal membranes broadly rounded to triangular covering about one-half the area of the stigma head; ovaries densely pubescent, rarely glabrate. *Follicles* unknown.

This species is known from the Atlantic lowlands from Panama through Costa Rica and into Nicaragua and apparently flowers from November through April.

BOCAS DEL TORO: Above Almirante, *Gentry 2806* (MO). COCLÉ: El Valle de Antón (N rim), *Allen 1644* (F, GH, MO, NY, US). COLÓN: Santa Rita (E) Ridge, *Duke 15247* (MO), *15248* (OS); *Dwyer & Gentry 9368* (MO); *Lewis et al. 5259* (DUKE, MO), *5373* (MO). PANAMÁ: Between Cerro Jefe and Eneida, *Dwyer et al. 8237* (MO).

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[10] *Fischeria panamensis* Spellman, sp. nov. Differt a speciebus affine calycis lobis lanceolati-acuminatis, plerumque quinquienis longioribus quam latioribus, marginibus distincte undulatis; lobis corollae ovalibus, eciliatis; ovariis dense pubescentibus raro glabratis.

12. MATELEA[11]

Matelea Aubl., Hist. Pl. Guiane Fr. 277, *t. 109*. 1775. TYPE: *M. palustris* Aubl.

Mostly perennial *herbs*, sometimes basally woody, usually scandent, but sometimes prostrate or erect, glabrous to densely ferruginous pubescent, the hairs frequently of two types, long multicellular ones which overtop shorter glandular ones. *Leaves* petiolate, variable in form but frequently cordate. *Inflorescence* usually umbelliform, commonly racemiform with age, few- to many-flowered, pedunculate. *Flowers* with the calyx 5-lobed nearly to the base, 5- or more glandular within at the base; corolla rotate to shallowly campanulate, usually green, sometimes brownish, shallowly or deeply 5-lobate; stamens inserted at the base of the corolla, the corona variable, entire or lobed, often annular and/or fimbriate, a faucal corona present or absent, the filaments connate into a short tube, the anthers not vesicular and lacking dorsal appendages; pollinia solitary in each anther theca, inserted horizontally or nearly so (sometimes appearing pendulous in those of quadrate form where the width equals or exceeds the length of the pollinium) with a conspicuous sterile, hyaline margin near the attachment to the translators; stigma usually broadly 5-angled and apically depressed. *Fruit* a single follicle, slender or broad, smooth, sometimes winged or with tuberculate projections.

This is a genus of 180–200 species ranging from the central United States southward into South America. The highly variable corona makes this one of the most interesting genera of the Asclepiadaceae, and it has been one of the primary criteria for the coining of some 50–60 separate generic names.

a. Mature leaves cordate at the base.
  b. Corolla suburceolate, the tube 1 cm long or more; leaves usually more than 12 cm long.
    c. Corolla lobes glabrous, dark chocolate brown ..... 3. *M. tristis*
    cc. Corolla lobes papillate-hispid, yellow-green to brownish-green ..... 2. *M. trianae*
  bb. Corolla rotate, the tube 5 mm long or less; leaves usually less than 12 cm long.
    d. Corolla less than 1 cm in diameter, the lobes reflexed at anthesis; stigma head circular.
      e. Stigma with a conspicuous peg-like beak ca. 2 mm long; stems and leaves with short, soft, white pubescence ..... 1. *M. maritima*
      ee. Stigma unappendaged; leaves and stems with long, spreading, red-brown hairs ..... 6. *M. pinguifolia*
    dd. Corolla more than 1 cm in diameter, the lobes spreading at anthesis; stigma head 5-angled.
      f. Corolla bright green; stems and leaves pubescent ..... 9. *M. viridiflora*
      ff. Corolla dull yellow-green to tan; stems and leaves glabrous or nearly so ..... 4. *M. pittieri*
aa. Mature leaves rounded to cuneate at the base, not cordate.
  g. Leaves and stems densely brown pubescent; leaves 10 cm or more long; flowers brown tinged with red or green.
    h. Flowers red-brown, corolla lobes spreading; pedicels less than 1 cm long ..... 7. *M. panamensis*
    hh. Flowers brownish-green; corolla lobes strongly reflexed; pedicels 2–3 cm long ..... 8. *M. brasiliensis*
  gg. Leaves and stems glabrous; leaves less than 10 cm long; flowers bright emerald green ..... 5. *M. mediocris*

[11] For a list of synonyms see Woodson (1941).

1. **Matelea maritima** (Jacq.) Woodson, Ann. Missouri Bot. Gard. 28: 222. 1941.

Cynanchum maritimum Jacq., Stirp. Amer. 83, *pl. 56*. 1763. TYPE: (not seen).
Gonolobus maritimus (Jacq.) R. Br., Mem. Wern. Soc. 1: 35. 1811.
G. floccosus Bertol., Opusc. 4: 521. 1823.
G. suberosus Spreng., Syst. 1: 846. 1825, non R. Br. TYPE: (not seen).
Ibatia maritima (Jacq.) Dcne. *in* DC., Prodr. 8: 599. 1844.
I. muricata Griseb., Fl. British W. Indies 421. 1861 TYPE: (not seen).
Lachnostoma maritimum (Jacq.) Nichols., Dict. Gard. 2: 236. 1884.

Slender pubescent *vines*; stems white pubescent. *Leaves* cordiform, acuminate, softly pubescent above and beneath; petiole 2–2.5 cm long; blade 4–6 cm long and 2.5–4 cm wide. *Inflorescences* sessile, few-flowered, umbelliform; pedicels stout, ca. 2 mm long, white pubescent. *Flowers* with calyx lobes ovate, acute, ca. 2 mm long and 1–1.5 wide, strigose outside, glabrous inside; corolla rotate, maroon to greenish-red, the lobes spreading or reflexed at anthesis, lanceolate, 4–5 mm long and ca. 2 mm wide, appressed white pubescent on both sides, less so above; corona cyathiform, thin, appearing fleshy, ca. 1 mm high, obscurely 5-lobed, each lobe bearing conspicuous white apical hairs; gynostegium depressed globose, ca. 1.1–1.2 mm high, slightly overtopping the corona; stigma head depressed, terminated by a peg-like appendage 1.4–1.8 mm long, this divided and minutely papillate at the apex. *Follicle* ovoid with a long acuminate apex, densely pubescent, irregularly covered with columnar tuberculate projections, each tubercle capped with a rounded mass of whitish spongy tissue, 5–7 cm long, 2–3 cm in diameter.

This species occurs at or near sea level from the Antilles into Venezuela, Colombia, and Panama.

COCLÉ: Aguadulce, near sea level, *Pittier 4888* (US). HERRARA: Las Salinas de Chitré on Bahia Parita, E of Chitré, *Croat 9694* (MO). Cienaga Juncallilo, near Correa, *McDaniel 8027A* (DUKE, FSU). LOS SANTOS: Monagre Beach, *Tyson et al. 3052* (MO). PANAMÁ: Near beach at Nueva Gorgona, *Duke 4526* (MO).

2. **Matelea trianae** (Dcne. *ex* Trin.) Spellman, comb. nov.

Macroscepis trianae Dcne. *ex* Trin., Compt. Rend. Hebd. Séances Acad. Sci. 74: 882. 1872. TYPE: Colombia, *Triana* (P, not seen).
M. barbata Blake, Contr. U. S. Natl. Herb. 20: 244. 1919. TYPE: Colombia, *Curran 182* (US).
M. panamensis Woodson, Ann. Missouri Bot. Gard. 26: 301. 1939. TYPE: Panama, *Woodson et al. 1228* (MO, NY, US).
Matelea stellulifera Standl. & L. O. Wms., Ceiba 1: 245. 1951. TYPE: Costa Rica, *Allen 5666* (F).

Coarse suffruticose *vines*, stems, petioles, and inflorescences densely covered with stiff, spreading, brownish hairs. *Leaves* narrowly to broadly ovate to suborbicular, shallowly cordate, densely pilose on both surfaces; petioles 4–7 cm long; blades 12–18 cm long and 5–14 cm wide. *Inflorescences* umbelliform, few- to several-flowered; peduncles 1–2 cm long; pedicels mostly ca. 1 cm long. *Flowers* large, somewhat foetid; calyx lobed to the base, the lobes lanceolate to ovate-lanceolate, acute, strigose outside, the margins ciliate, 10–12 mm long and 5–8 mm wide; corolla pale yellowish-green becoming brownish-green, salverform, short pubescent outside, the tube constricted at the mouth, 9–12 mm long, the

lobes ovate to suborbicular, hispidulous-papillate inside, especially near the mouth, 9–12 mm long, nearly as wide; corona of 5 distinct fleshy segments, the apices nearly quadrate and equaling the corolla tube or slightly exserted. *Follicles* (described from Colombian material) attenuate-ovoid, inserted obliquely on the fruiting pedicel, ca. 11 cm long, 3 cm in diameter, conspicuously 7-winged, the wings extending the full length of the fruit.

As here conceived, *M. trianae* ranges from the northern part of Costa Rica along the Pacific side of the continent into western Colombia and into the Atlantic lowlands of Venezuela.

Both this and the following species belong to subgenus *Macroscepis*, a group in need of critical study. The closely related *Matelea urceolata* (Karst.) L. O. Wms., of Colombia and Venezuela, may also occur in Panama. It is distinguished by the long flattened hairs of its corolla lobes and by a 7-winged fruit in which the lateral wings do not extend the full length of the follicle.

CANAL ZONE: Road C2F, ½ mi. NW of Summit Naval Radio Station, *Croat 11028* (MO). COCLÉ: Aguadulce, in savannahs near sea level, *Pittier 4940* (US). DARIÉN: Without locality, *Dawe 875* (NY). LOS SANTOS: Headwaters of Río Pedregal, 25 mi. SW of Tonosí, *Lewis et al. 2971* (F, MO). PANAMÁ: Near Capira, *Woodson et al. 1228* (MO, NY, US). Panamá Viejo, *Duke 5723A* (MO). Road toward top of Cerro Campana, *Duke 5966* (G, MO). Isla Tobago, *Woodson et al. 1432* (F, G, MO, NY). San José Island, Area 11 A, *Johnston 1056* (G, MO). VERAGUAS: Above Santa Fé on slopes of Cerro Tute, *Gentry 6221* (F, MO).

3. **Matelea tristis** (Seem.) Spellman, comb. nov.

Schubertia tristis Seem., Bot. Voy. Herald 160. 1852–57. TYPE: Panama, Veraguas, *Seemann 158* (BM, not seen; MO, photo).
Macroscepis tristis (Seem.) Benth. & Hook. f. *ex* Hemsl., Biol. Cent. Amer. Bot. 2: 321. 1882.

Scandent *shrub*, more or less hirsute with the exception of the corolla and inside of the calyx, the hairs dark brown. *Leaves* opposite, ovate, cordate, cuspidate, generally (including the petiole) 15 cm long and from 8–10 cm wide; petiole 2.5 cm long. *Inflorescence* umbellate, few-flowered. *Flowers* with calyx lobes ovate, acuminate, as long as the corolla tube; corolla salverform, the tube ca. 12 mm long, constricted at the mouth, light brown, the lobes dark chocolate brown, giving the flowers a dull appearance, ovate, obtuse, equaling the tube. *Follicles* unknown.

Known only from the type collection, which I have not seen. The above description was derived from Seemann's original description and from a photograph of the type. *Matelea tristis* may be a synonym of *Matelea hirsuta* (Vahl) Woodson, an Antillean species.

VERAGUAS: Río de Santa María, between Santiago de Veraguas and Natá, *Seemann 158* (BM, not seen; MO, photo).

4. **Matelea pittieri** (Standl.) Woodson, Ann. Missouri Bot. Gard. 28: 234. 1941.

Vincetoxicum pittieri Standl., Field Mus. Publ. Bot. 17: 270. 1937. TYPE: Panama, *Pittier 3059* (F, US).
V. discolor Woodson, Ann. Missouri Bot. Gard. 25: 833, *fig. 1*. 1938. TYPE: Panama, *Allen 322* (MO).

Herbaceous or subligneous *vines*; stems glabrous or nearly so. *Leaves* ovate to subcordate, glabrous, apically acuminate, basally rounded, cordate when mature, 7–12 cm long and 3.5–7 cm wide; petioles 2–2.5 cm long. *Inflorescences* racemose, fewer than 10-flowered, glabrous or puberulent throughout; peduncles 2–5 cm long; pedicels 1–2.5 cm long. *Flowers* with the calyx divided to the base, the lobes lanceolate, 3–4 mm long and 1.5–2 mm wide, brownish puberulent outside, glabrous inside; corolla rotate-subcampanulate, 2.5–3 cm in diameter, yellowish-green or tan with darker green reticulations, the lobes broadly ovate, apically acute or obtuse, 7–11 mm long, 6–10 mm wide, glabrate apically, white pilose basally on the inside, papillate outside; corona of 5 fleshy, thick, ± ligular segments joined near the base; gynostegium ca. 2–3 mm high; stigma head pentagonal, flat, covered by a thick membrane. *Fruit* unknown.

The species is known only from Panama at elevations above 1200 m. *Matelea pittieri* Woodson and *M. tinctoria* Woodson from Costa Rica may be synonyms of *M. picturata* (Hemsl.) Woodson from Guatemala, in which case *M. picturata* would be the correct name. All 3 are from similar elevations, and they are separated by minor differences. Further study may resolve this question.

CHIRIQUÍ: Trail from Bambito to Cerro Punta, *Allen 322* (MO). Trail from Paso Ancho to Monte Lirio, *Allen 1479* (F, MO, US). Boquete, *Davidson 858* (F, MO, US). Forests along the Río Ladrillo and vicinity, above El Boquete, *Pittier 3059* (F, US).

5. **Matelea mediocris** Woodson, Fieldiana: Bot. 28: 510. 1953. TYPE: Venezuela, Bolivar, *Steyermark 60690* (F, MO).

Slender *vines*; stems glabrous or glabrate except for minute hairs at the nodes. *Leaves* broadly lanceolate to ovate, glabrous, dark green and shiny above, lighter beneath, apically rounded and submucronate, basally rounded to nearly cuneate, mostly 6.5–12 cm long and 3–5.5 cm wide; petioles 7–12 mm long. *Inflorescences* racemose, fewer than 10-flowered; peduncles 2–4 mm long; pedicels 5–10 mm long. *Flowers* small, calyx lobes glabrate, lanceolate-ovate, ca. 1.5–2 mm long and 1 mm wide; corolla rotate, green with darker prominent veins, glabrous throughout, 8–9 mm in diameter, lobes reflexed at anthesis, ovate, 3–4 mm long and 2–3 mm wide; corona fleshy, annular, broadly 5-lobed; gynostegium 1.5–2 mm high; stigma head brownish in color, pentagonal, slightly domed. *Fruit* not known.

The two collections cited below represent the most northward extension of a small species complex of 3-5 taxa which includes the type of the genus. All are small glabrous vines with small green flowers, and as a group they are relatively common in Northern Brazil, Amazonian Peru, Colombia, Venezuela, and the Guianas.

COLÓN: Santa Rita Ridge, *Gentry & Dwyer 4814* (MO). PANAMÁ: La Eneida, ca. 16 km E of Cerro Azul (Goofy Lake), *Dressler 4315* (MO).

6. **Matelea pinguifolia** (Standl.) Woodson, Ann. Missouri Bot. Gard. 28: 235. 1941.—FIG. 12.

Vincetoxicum pinguifolium Standl., Jour. Washington Acad. Sci. 17: 13. 1927. TYPE: Panama, *Standley 40946* (US).

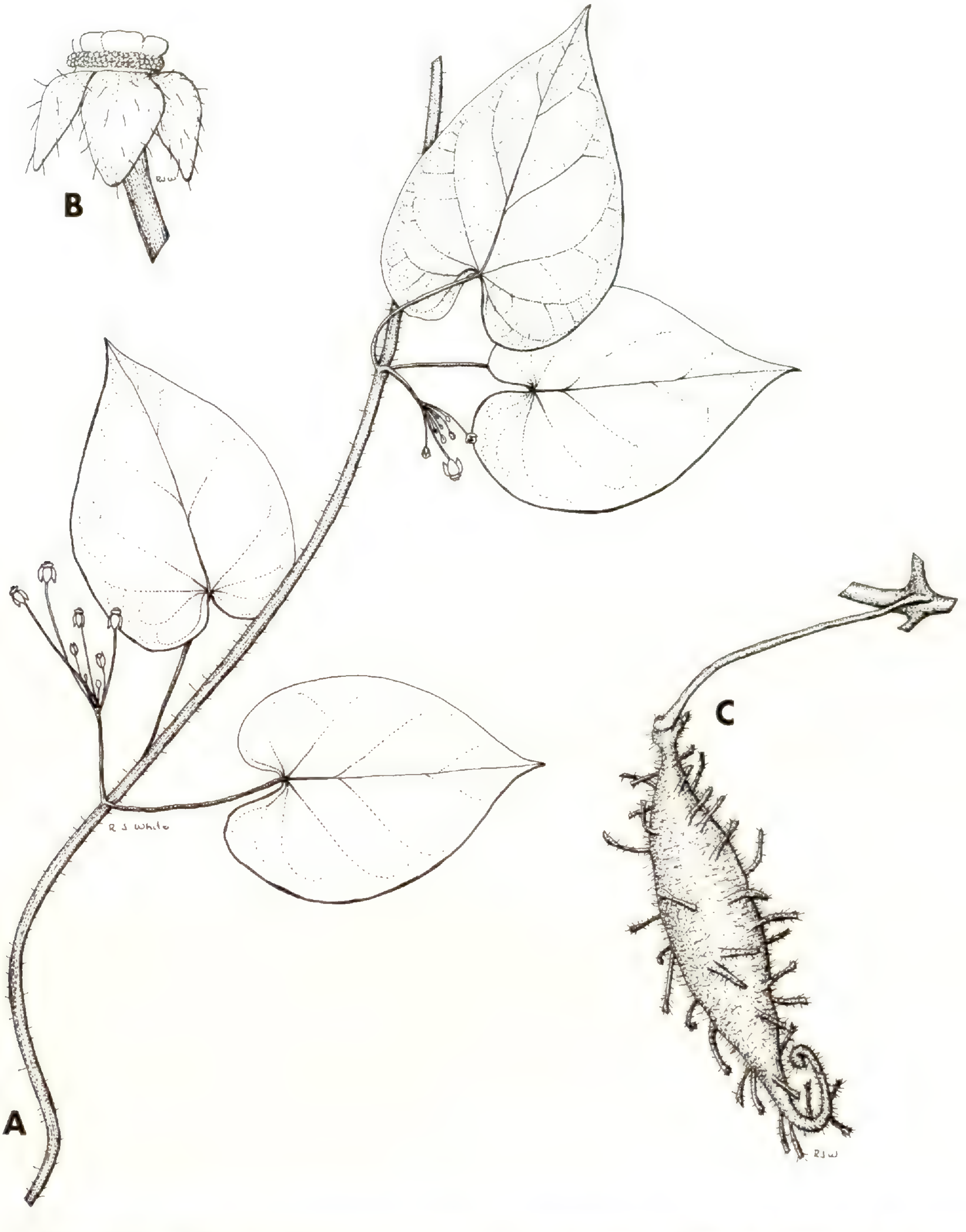


FIGURE 12. *Matelea pinguifolia* (Standl.) Woodson.—A. Flowering stem (× ⅗).—B. Flower (× 3). [After *Allen 2036* (MO).]—C. Fruit (× ⅗). [After *Dwyer 2185* (MO).]

Herbaceous or subligneous *vines*; stems pubescent, the hairs of 2 types, short bulbous ones overtopped by brown, multicellular, stiff ones to 3 mm in length which decrease in density with age. *Leaves* broadly ovate-cordate, acuminate, glabrate to densely puberulent beneath, puberulent above, 6–10 cm long and 3–7 cm wide; petioles slender, 2–6 cm long. *Inflorescences* racemiform, 10–20-

flowered, minutely brown puberulent; peduncles 1–1.5 cm, occasionally to 3 cm long; pedicels mostly 2–3 cm long. *Flowers* with the calyx lobes lanceolate-ovate to ovate, glabrous inside, brownish puberulent outside, 2–4 mm long and 1.5–2.5 mm wide; corolla brownish to orange, the lobes strongly reflexed at maturity, ovate to elliptic, puberulent outside, inner (adaxial) surface with long whitish hairs along the margin and near the apex, occasionally scattered over the entire surface, 4–6 mm long and 2–3 mm wide; corona fleshy, annular, the surface corrugated, purplish-black, 1.5–2 mm high; gynostegium slightly exceeding the corona in height; stigma head round or obscurely 5-angled. *Follicles* narrowly ovoid with a slender acuminate apex, 10–12 cm long, ca. 2 cm in diameter, tuberculate, pubescent, the tubercles long and slender, to 1.5 cm long, the pubescence of brownish, multicellular hairs up to 6 mm long.

The peculiarly colored flowers with their conspicuous corona and distinctive follicles make this one of the most easily identified milkweeds in Panama. It is known only from Colombia, Panama, and Costa Rica. While the Colombian collection agrees with the Panamanian material, a single collection (*Brenes 1450*) from near San Ramón, Costa Rica, is noticeably different in its overall dense pubescence, particularly the presence of long brown hairs on the inflorescence and calyx. Material from Chiriquí (*Tyson 5860*) is somewhat intermediate between typical material and the Costa Rican collection.

CANAL ZONE: Madden Dam, *Dwyer 2185* (MO). Barro Colorado Island, *Shattuck 612* (F, MO), *727* (MO); *Standley 40871, 40946, 41116* (all US). CHIRIQUÍ: Opening to canyon to Bambito, 5000 ft, *Tyson 5860* (DUKE, FSU, MO). PANAMÁ: Near Pacora, *Allen 2036* (F, MO, US). Forest from first sharp bend on Río Pasiga, 0–2.5 mi. along lumber road to Río Maestro, *Gentry 2347* (MO).

7. **Matelea panamensis** Spellman & Dwyer, Ann. Missouri Bot. Gard. 60: 568, *fig. 1.* 1973. TYPE: Panama, *Dwyer 8300* (MO).

Vines; stems terete, densely pubescent, the pubescence of 2 types, the short, sometimes bulbous hairs overtopped by stiff, brown, spreading, multicellular ones 3–5 mm long. *Leaves* elliptic, basally obtuse, truncate, or shallowly cordate, discolorous, pubescent on both surfaces, 10–15 cm long and 7–10 cm wide; petioles 3–6 cm long. *Inflorescences* umbelliform, pubescent as on the stems, ca. 10-flowered, but only 2 usually open at a time; peduncles ca. 2 cm long; pedicels ca. 1.5 cm long. *Flowers* greenish or purplish brown; calyx lobes lanceolate, densely brown pubescent outside, glabrous inside, 5–6 mm long and 2–3 mm wide; corolla rotate to shallowly campanulate, 2–3 cm in diameter, the lobes broadly ovate, 6–9 mm long and wide, with inconspicuous short pubescence inside and outside as on the stems, but with the long hairs mostly in a thin band at the base of the lobes, a faucal annulus present as a low thin ridge of tissue, ca. 0.1 mm high, densely but minutely white pubescent; corona carnose, 5-lobed, the lobes connected by a narrow annular band of tissue, the apically thickened part of the lobe broadly reniform, ca. 1 mm long and 1.5 mm wide; gynostegium ca. 2 mm high; stigma head broadly pentagonal, slightly depressed, covered by a prominent thick white membrane. *Follicles* subovoid, ca. 20 cm long, 9 cm in diameter, the exocarp woody with a low, short dorsal ridge.

Known only from Panama, this species represents the most northward extension of a small group of taxa which would formerly have been placed in the genus *Phaeostemma*. Other members of this group are known from Colombia, Peru, Ecuador, and Bolivia.

COCLÉ: Cerro Pilón, *Dwyer 8300* (MO). PANAMÁ: 0.5 mi. beyond the cattle shute, Cerro Jefe, *Gentry 4884* (MO).

8. **Matelea brasiliensis** (Schltr.) Spellman, Phytologia 25: 438. 1973.

Fimbristemma brasiliensis Schltr., Notizbl. 6: 178. 1914. TYPE: Brazil, *Ule 9529* (not seen).

Vines with dense, spreading, brown pubescence throughout; stems terete, pubescence to 2 mm long, the hairs stiff, multicellular. *Leaves* elliptic to ovate, apically short acuminate, basally obtuse to subcordate, discolorous, both surfaces densely brown-pubescent, 9–15 cm long and 5–9 cm wide; petioles 1–2 cm long. *Inflorescences* umbelliform, ca. 20-flowered, subsessile; the peduncles not exceeding 2 mm; pedicels 2–3 cm long. *Flowers* with the calyx lobes lanceolate, densely pubescent on the outside, glabrous within, 2.5–3 mm long and ca. 1 mm wide; corolla lobes reflexed at maturity, greenish-brown or tan with dull green reticulations, elliptic, apically rounded, the outer (abaxial) surface with long multicellular hairs, the inner surface minutely puberulent, 7–8 mm long and 2.5–3.5 mm wide; corona fleshy, cyathiform, 2.5–3.5 mm high, shallowly 5-lobed; gynostegium equaling or slightly shorter than the corona; stigma head broadly pentagonal, ca. 3 mm in diameter, slightly depressed. *Follicles* unknown.

Aside from the following collection, the species is known from only two localities, the type locality in Brazil and a single locale in Peru.

PANAMÁ: Between Cerro Jefe and Eneida, 2100–2700 ft, *Dwyer et al. 8218* (MO).

9. **Matelea viridiflora** (Meyer) Woodson, Ann. Missouri Bot. Gard. 28: 235. 1941.—FIG. 13.

Cynanchum viridiflorum Meyer, Prim. Fl. Esseq. 141. 1818. TYPE: British Guiana, *Hamburg* (not seen).
Gonolobus viridiflorus (Meyer) Roem. & Schult. *in* L., Syst. Veg., ed. 15. 6: 61. 1819.
Vincetoxicum viridiflorum (Meyer) Standl., Jour. Washington Acad. 17: 14. 1927.

Herbaceous *vines*; stems slender, pubescent, trichomes multicellular, brownish, to 1.5 mm long. *Leaves* ovate to elliptic, acuminate apically, shallowly cordate, the sinuses open, or frequently the basal lobes imbricate, sparsely strigose on both sides and the margins, discolorous, mostly 5–11 cm long and 2.5–5 cm wide; petioles slender, pubescent, mostly 2–4 cm long. *Inflorescences* racemiform, ca. 10-flowered, minutely pubescent; peduncles 5–10 mm long; pedicels 1.5–2.5 cm long. *Flowers* green; calyx lobes lanceolate, glabrate on both sides, ciliate, 4–5 mm long and 2–3 mm wide; corolla rotate, 2–3 cm in diameter, lobes with prominent reticulations of darker green, ovate to elliptic, obtuse, 8–15 mm long and 5–9 mm wide, glabrous to weakly strigose within, glabrous outside, a faucal annulus present but interrupted, consisting of 5 small mounds of tissue opposite the sinuses, each mound densely puberulent; corona inconspicuous, 5-lobed; gynostegium 1–2 mm high; stigma head yellow or brownish-yellow, broadly

FIGURE 13. *Matelea viridiflora* (Meyer) Woodson.—A. Flowering stem (× 3/5).—B. Flower (× 1⅘). [After *Croat 6102* (MO).]—C. Fruit (× 3/5). [After *Johnston 1310* (MO).]

pentagonal. *Follicles* ovoid-acuminate ca. 2 cm in diameter, glabrous, smooth except for 5 low, longitudinal wings, 4–7 cm long.

This species ranges from eastern Brazil, the Guianas, Venezuela, Ecuador, and Colombia through Panama and into Costa Rica. *Matelea viridiflora* must be thought of as intermediate between *Matelea* and *Gonolobus*. There appear to be minute anther appendages associated with *M. viridiflora*, and the fruit appears to fit into the *Gonolobus* rather than the *Matelea* group. Until more information is available, it is better to maintain the present status of the taxon.

BOCAS DEL TORO: Water Valley, Chiriquí Lagoon, *Wedel 1826* (MO). CANAL ZONE: Pipeline Road 6 mi. NW of Gamboa gate, *Croat 12760* (DUKE, MO). Near beach at Ft. Kobbe, *Duke 4179* (MO). Road C-21, *Duke 5776* (MO). Balboa, *Standley 25607* (US).

Mandinga, *Stevens 1358* (US). W slope of Ancon Hill, *Woodson et al. 715* (MO). Barro Colorado Island, *Croat 6102, 12882, 16630* (all MO); *Foster 1965* (DUKE); *Shattuck 727* (F, MO). CHIRIQUÍ: Road to Boquete near David, *D'Arcy & D'Arcy 6286* (MO). Near San Félix, *Pittier 5235* (US). DARIÉN: Near Yapé, *Allen 858* (US). Sambu River above tide limit, *Pittier 5543* (US). PANAMÁ: Tocumen, *Dwyer 2576, 5099* (both MO). Las Sabanas, *Heriberto 268* (US). Cerro Campana, *Lewis et al. 3083* (F, MO). San José Island, *Johnston 845* (MO, US), *1310* (MO). VERAGUAS: Above Santa Fé on slopes of Cerro Tute, below Agricultural School, *Gentry 6201* (MO).

13. GONOLOBUS

Gonolobus Michx., Fl. Bor.-Amer. 1: 119. 1803. TYPE: *G. gonocarpos* (Walt.) Perry.

Vincetoxicum Walt., Fl. Carol. 13, 104. 1788, *non* Moench, 1794. TYPE: *V. gonocarpum* Walt.
Exolobus Fourn. *in* Mart., Fl. Bras. 6(4): 318. 1885. TYPE: *E. patens* (Dcne.) Fourn.

Herbaceous or semi-woody *vines*, scandent or sometimes prostrate, variously pubescent or glabrate. *Leaves* petiolate, usually cordate, sometimes rounded or cuneate basally, glabrous or pubescent. *Inflorescence* umbelliform or racemiform, pedunculate or subsessile, usually few-flowered. *Flowers* green, rarely reddish, yellow or white; calyx 5-parted, usually with a single gland at the base of each sinus within; corolla rotate to subcampanulate, the tube usually short, the lobes linear to suborbicular, contorted in bud, the faucal annulus inconspicuous or prominent, usually ciliate; stamens inserted at the base of the corolla, the corona inconspicuous or prominent, carnose, usually 5-lobed, the filaments forming a short tube, the anthers short and broad, dorsally appendaged, the appendages fleshy, usually conspicuous, laminate, variable in form, entire to bi- or trifurcate; pollinia solitary in each theca, inserted horizontally or nearly so, ovoid to pyriform, conspicuously excavated on one face and with a sterile hyaline portion near the attachment of the translators; stigma apically depressed, sharply 5-angular. *Follicles* variously shaped, usually glabrous, smooth, tuberculate, or winged; seeds comose.

A genus of about 100 species, *Gonolobus* is indigenous to North America, primarily Mexico. As with most asclepiadaceous genera, *Gonolobus* is in need of revision. In Panama, the genus is most easily recognized by the sharply pentagonal stigmas and laminate anther appendages.

Gonolobus billbergianus Beurling, Kongl. Vet. Akad. Handl. 1854: 138. 1855, is based on a Billberg collection which has not been seen. The species is described as having erect, long, dark brown hairs on the stems as well as stiffly pubescent leaves and flowers which indicates that it may be a *Matelea* or *Fischeria*. It cannot be identified in the Panamanian flora today.

a. Corolla conspicuously hispid-barbellate within ..... 7. *G. edulis*
aa. Corolla glabrous to glabrate within, not hispid-barbellate.
  b. Corolla lobes to 2.5 cm long, minutely white papillate along one margin ..... 1. *G. albomarginatus*
  bb. Corolla lobes mostly less than 2 cm long, not white papillate along one margin.
    c. Anther appendages with a pair of lateral lobes or a central bifurcate lobe.
      d. Appendages with short rounded lateral lobes ..... 8. *G. lewisii*
      dd. Appendages with long, central bifurcate lobes ..... 3. *G. ophioglossa*

cc. Anther appendages unlobed.
e. Leaves acute, rounded, or truncate at the base.
f. Corolla less than 1 cm in diameter ..... 6. *G. fuscoviolaceus*
ff. Corolla 1.5–2.5 cm in diameter ..... 5. *G. chiriquensis*
ee. Leaves cordate at the base.
g. Calyx lobes ca. 1 cm long; anther appendages subquadrate .... 4. *G. allenii*
gg. Calyx lobes ca. 0.5 cm long; anther appendages suborbicular ..... 2. *G. inaequalis*

1. **Gonolobus albomarginatus** (Pittier) Woodson, Ann. Missouri Bot. Gard. 28: 242. 1941.—FIG. 16A.

Exolobus albomarginatus Pittier, Contr. U. S. Natl. Herb. 13: 108, *fig. 16.* 1910. TYPE: Costa Rica, Limon Prov., *Pittier* (US 573016, not seen).

Herbaceous or subligneous *vines*; stems slender, sparsely to densely pubescent, the hairs stiff, spreading. *Leaves* ovate to oblong-ovate, apically acuminate, deeply cordate at the base, short strigose to glabrate on both sides, 6–16 cm long and 3–8 cm wide; petioles glabrate to short pubescent, 3–6 cm long. *Inflorescences* umbelliform racemose, fewer than 10-flowered, puberulent throughout; peduncles 1–2 cm long; pedicels 2.5–4 cm long. *Flowers* with the calyx divided to the base, the lobes lanceolate to linear-lanceolate, pubescent outside, glabrous within, 8–15 mm long and 2–4 mm wide; corolla green with darker reticulations inside, rotate, 2.5–4 cm in diameter, the lobes lanceolate, acute, 15–25 mm long and 3–5 mm wide, puberulent outside, glabrous inside except for a band of dense white papillae along one margin, the faucal annulus a prominent ridge of corolline tissue nearly 1 mm high, ciliate throughout or in tufts opposite the corolla sinuses; corona carnose, obscurely 5-lobed, the margins crenulate; the anther appendages subquadrate, remotely emarginate or occasionally tridentate, 1–2 mm long and 1–2 mm wide at the base; stigma head sharply pentagonal. *Follicles* unknown.

Known only from Costa Rica, Panama, and western Colombia, *G. albomarginatus* is closely related to and possibly conspecific with *G. uniflorus* H.B.K. and *G. leianthus* (Donn. Sm.) Woodson from Mexico and Guatemala.

BOCAS DEL TORO: Changuinola Valley, *Dunlap 353* (F, US). Chiriquicito to 5 mi. S along Río Guarumo, *Lewis et al. 2079* (F, MO). Water Valley, Chiriquí Lagoon, *Wedel 1631, 1704, 1752* (all MO, US). CANAL ZONE: Around Gamboa, *Pittier 4810* (US). COCLÉ: El Valle de Antón, *Allen 3701* (MO). El Valle de Antón, trails near Finca Tomas Arias, *Allen 4225* (MO). Road ca. 8 mi. N of El Valle de Antón, *Luteyn & Kennedy 1700* (DUKE, MO).

2. **Gonolobus inaequalis** L. O. Wms., Ann. Missouri Bot. Gard. 55: 49. 1968. TYPE: Panama, *Allen 2031* (MO, holotype; F, US, isotypes).—FIG. 16F.

Herbaceous *vines*; stems glabrous to hirsute. *Leaves* ovate to elliptic, apically acuminate, basally cordate, glabrous to sparsely pubescent, 5–11 cm long and 2–5 cm wide; petioles sparsely hirsute, 3–6 cm long. *Inflorescences* contracted racemose, mostly 1–5-flowered; peduncles pilose, 1–3 cm long; pedicels glabrate, mostly 2–4 cm long. *Flowers* with the calyx divided nearly to the base, the lobes nearly linear to lanceolate, 3–6 mm long and 1.5–2.5 mm wide, glabrous inside and out; corolla rotate, green, 2.5–4 cm in diameter, the lobes lanceolate-ovate,

noticeably unequal in length, 11–17 mm long and 4–6 mm wide, glabrous throughout, the faucal annulus an inconspicuous, frequently interrupted ridge, sometimes manifest only as 5 small mounds opposite the sinuses of the corolla, glabrous; anther appendages with a central suborbicular lobe which is ca. 1.5 mm long and 1 mm wide; the corona thick-carnose, 5-lobed, the lobes broadly rounded, the margins somewhat undulate; gynostegium pentagonal; stigma head depressed. *Follicles* unknown.

Now known from Panama and Colombia, the species is conspicuous for its tendency towards zygomorphy. This condition is occasional in *Gonolobus*, but seems to be a constant feature of *G. inaequalis*. Future studies may show this taxon to be conspecific with or at least closely related to *G. eriocladon* Benth. from Colombia. There is no authentic material available for comparison, and the taxon is apparently known only from the type, a Hartweg collection which is housed at Kew.

CANAL ZONE: Near Madden Dam, *Allen 2010* (MO, US). Palo Seco, *Allen 2249* (MO). PANAMÁ: Near Pacora, *Allen 2031* (F, MO, US). Cerro cerca de Puebla de Veracruz, *Caballero 20* (MO). Forest near dam site S of Cañita, *Croat 14507* (MO). Without locality, *Dwyer 4043* (US). Agric. Exp. Sta. at Matías Hernández, *Pittier 6809* (US).

3. **Gonolobus ophioglossa** Woodson, Ann. Missouri Bot. Gard. 29: 366. 1952. TYPE: Panama, *Allen 2366* (MO, holotype; US, isotype).—FIG. 16E.

Herbaceous *vines*; stems sparsely pilose in lines or glabrate. *Leaves* lanceolate to lanceolate-elliptic, apically acuminate, basally acute, truncate, or shallowly cordate, glabrous or glabrate on both surfaces, mostly 5–10 cm long and 2–4 cm wide; petioles pilosulose to glabrous, 1–3 cm long. *Inflorescences* umbelliform racemose, sometimes bifurcately branched, 5–10-flowered or sometimes twice that number in branched inflorescences, glabrous or nearly so throughout; peduncles 5–10 mm long; pedicels slender, 1.5–3.5 cm long. *Flowers* glabrous throughout; calyx lobes linear-lanceolate to lanceolate, 3–5 mm long and 1–2 mm wide; corolla rotate, green, 2.6–4 cm in diameter, divided nearly to the base, the lobes narrowly to broadly elliptic, 13–19 mm long and 7–9 mm wide, the faucal annulus a thin, broadly 5-angled ridge ca. 0.5 mm high, usually with a triangular group of papillae extending from the angles to the sinuses of the corolla, otherwise glabrous, rarely with the papillae lacking; anther appendages with a central linear appendage which is bifurcate at the apex, the bifurcate lobes usually extended at right angles to the base of the appendage and ca. 0.7 mm long, the non-divided basal portion ca. 0.9 mm long and 0.6 mm wide; the corona thin, fleshy, shallowly 5-lobed, the lobes broadly rounded to triangular, the margins erose-crenulate; gynostegium pentagonal; stigma head slightly depressed. *Follicles* unknown.

Known only from Panama, this species is distinguished from other members of the genus by its glabrous flowers and bifurcate anther appendages.

BOCAS DEL TORO: Between Buena Vista coffee finca and Cerro Pilón on Chiriquí Trail, *Kirkbride & Duke 694* (MO). COCLÉ: Near La Mesa, N of El Valle de Antón, *Allen 2366* (MO, US). Hills below Cerro Pilón (above El Valle de Antón), *Croat 14404* (MO). PANAMÁ: Cerro Jefe, *Dressler 3823* (MO).

4. **Gonolobus allenii** Woodson, Ann. Missouri Bot. Gard. 27: 333, *fig. 1.* 1940. TYPE: Panama, *Allen 1831* (MO, US).—FIG. 16B.

Herbaceous *vines*; stems sparsely short pilose. *Leaves* ovate to elliptic, basally cordate, apically acuminate, 5–10 cm long and 2–4 cm wide, sparsely pubescent on both sides; petioles pilosulous, 2–4 cm long. *Inflorescences* racemiform, 2–4-flowered, pilosulous throughout; peduncles 1–2 cm long; pedicels 2–3 cm long. *Flowers* with the calyx lobes linear lanceolate, sparsely pilose outside, glabrous within, 6–10 mm long and 1.5–3 mm wide; corolla rotate, green, 3–4 cm in diameter, the lobes lanceolate-ovate, 13–14 mm long and 8–9 mm wide, papillate beneath, glabrate above, remotely papillate along one margin, the faucal annulus circular, ciliate; corona fleshy, shallowly 5-lobed, the lobes broadly rounded, the margins rugose-fimbriate; anther appendages subquadrate, ca. 1.2 mm long and 1.4 mm wide; stigma head pentagonal. *Follicles* unknown.

Known only from Panama, *G. allenii* is doubtfully distinct from *G. albomarginatus* and may represent an ecological variant of the latter.

CANAL ZONE: Barro Colorado Island, *Wetmore & Abbe 202* (F, MO). COCLÉ: N rim of El Valle de Antón, *Allen 1831* (MO, US). PANAMÁ: 4 km del corregimiento de Pacora, *Carrera 31* (MO).

5. **Gonolobus chiriquensis** (Woodson) Woodson, Ann. Missouri Bot. Gard. 28: 462. 1941.—FIG. 14.

Vincetoxicum chiriquense Woodson, Ann. Missouri Bot. Gard. 24: 199. 1937. TYPE: Panama, *Seibert 231* (MO).

Herbaceous *vines*; stems slender, glabrous or nearly so. *Leaves* narrowly ovate to elliptic, apically acuminate, basally truncate to rounded at maturity, glabrous, 4–14 cm long and 2–5 cm wide; petioles glabrous, 2–5.5 cm long. *Inflorescences* umbelliform, mostly 2–6-flowered, glabrous throughout; peduncles 1–3 cm long; pedicels mostly 1–2 cm long. *Flowers* with the calyx glabrous, the lobes lanceolate-elliptic to lanceolate, 4–5 mm long and 1–2 mm wide; corolla rotate, green, 1.7–2.5 cm in diameter, the lobes broadly ovate, 6–10 mm long and 5–8 mm wide, glabrous outside, puberulent along one margin within, the faucal annulus a remotely 5-angled, indistinct, glabrous ridge of tissue; anther appendages basically rounded but with a short mamillate tip projecting centrally from them, ca. 0.9 mm long and 1.2 mm wide at the base; corona thick-carnose, 5-lobed, the lobes pectinate-rugose along their margins; gynostegium pentagonal; the stigma head strongly depressed. *Follicles* unknown.

Known only from Panama at elevations above 1000 m, this taxon and the related *G. fuscoviolaceus* are distinctive in their nearly complete lack of pubescence. They are distinguished from each other by the much smaller flowers of *G. fuscoviolaceus* and its cordate rather than truncate to rounded leaf bases.

CHIRIQUÍ: Trail from Cerro Punta to headwaters of Río Caldera, *Allen 1448* (MO, US). Near Punto, *Allen 3498* (MO). Near Monte Lirio, Valley of upper Río Chiriquí Viejo, *Seibert 231* (MO); *White 64* (MO). Quebrado Velo, *Woodson & Schery 274* (MO, US). Near Bajo Mona and Quebrado Chiquero, *Woodson & Schery 520* (MO, US); *Woodson et al. 998* (MO).

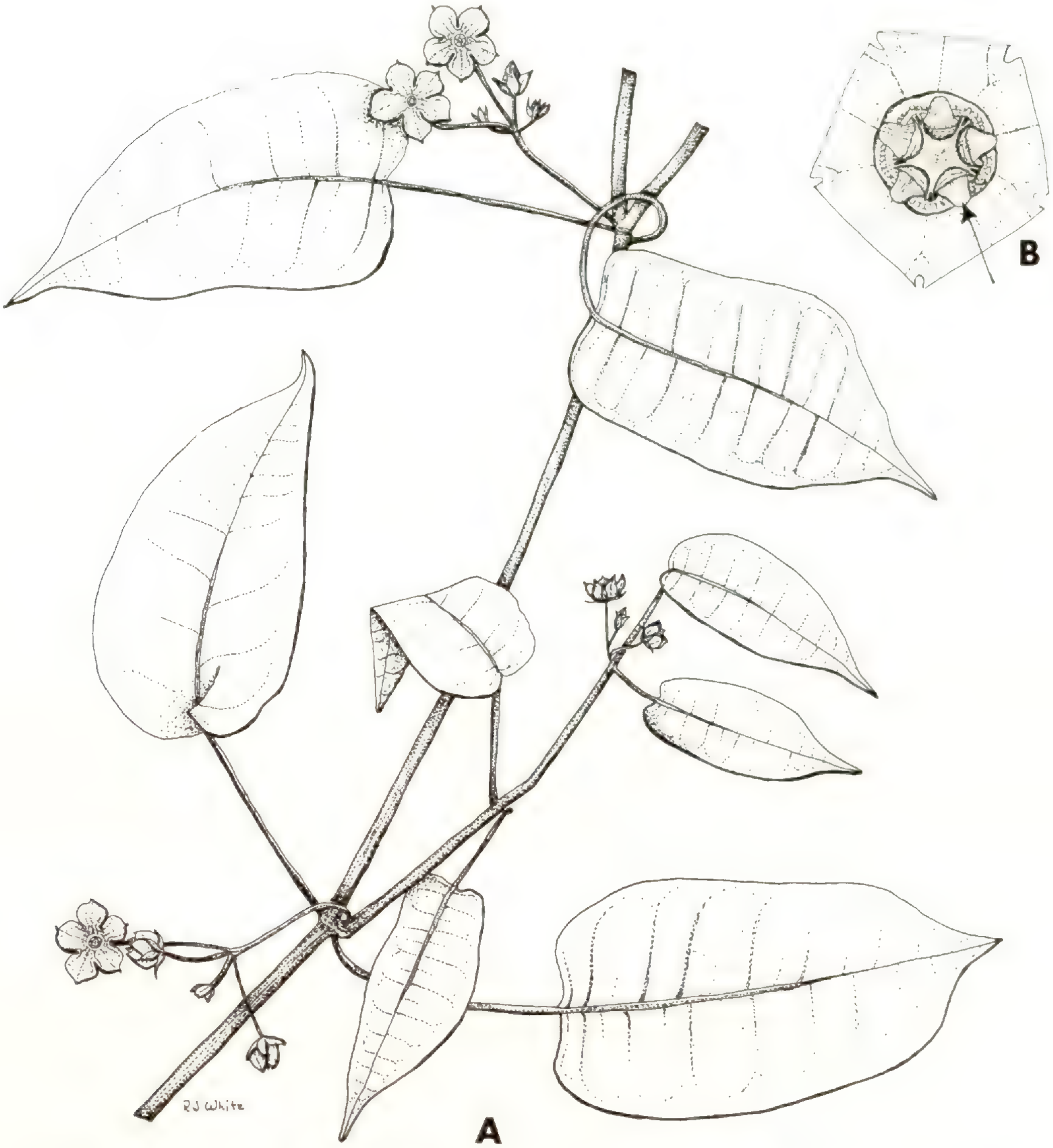


FIGURE 14. *Gonolobus chiriquensis* (Woodson) Woodson.—A. Flowering stem ($\times \frac{3}{5}$). —B. Central part of flower showing gynostegium, anther appendage marked with arrow .($\times 6$). [After *Allen 1448* (MO).]

6. **Gonolobus fuscoviolaceus** Woodson, Ann. Missouri Bot. Gard. 28: 462. 1941. TYPE: Panama, *Woodson & Schery 695* (MO, US).—FIG. 16D.

Herbaceous *vines*; stems slender, glabrous. *Leaves* lanceolate to lanceolate-elliptic, acuminate apically, basally rounded to subcordate, discolorous, glabrous, mostly 5–10 cm long and 2–4 cm wide; petioles glabrous, 1.5–2.5 cm long. *Inflorescences* umbelliform racemes, mostly 7–12-flowered, glabrate throughout; peduncles 10–12 mm long; pedicels 6–8 mm long. *Flowers* with the calyx lobes glabrous, lanceolate, 2–2.5 mm long and 1–1.5 mm wide; corolla rotate, green, 7–8 mm in diameter, the lobes ovate, 2.5–3 mm long and 2–2.5 mm wide, glabrous

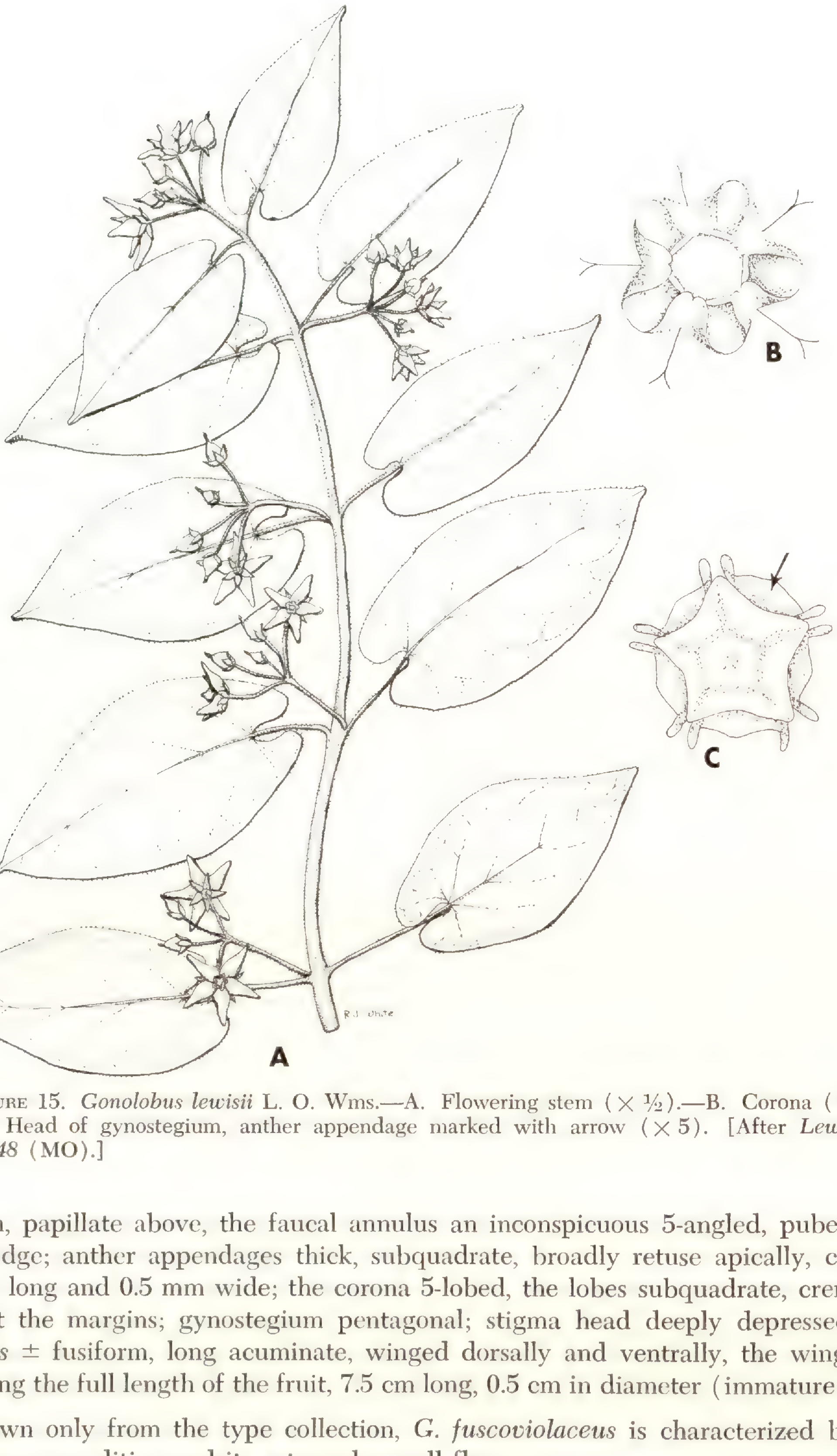


FIGURE 15. *Gonolobus lewisii* L. O. Wms.—A. Flowering stem (× ½).—B. Corona (× 5).—C. Head of gynostegium, anther appendage marked with arrow (× 5). [After *Lewis et al. 2248* (MO).]

beneath, papillate above, the faucal annulus an inconspicuous 5-angled, puberulent ridge; anther appendages thick, subquadrate, broadly retuse apically, ca. 0.3 mm long and 0.5 mm wide; the corona 5-lobed, the lobes subquadrate, crenulate at the margins; gynostegium pentagonal; stigma head deeply depressed. *Follicles* ± fusiform, long acuminate, winged dorsally and ventrally, the wings extending the full length of the fruit, 7.5 cm long, 0.5 cm in diameter (immature).

Known only from the type collection, *G. fuscoviolaceus* is characterized by its glabrous condition and its extremely small flowers.

CHIRIQUÍ: Near Bajo Chorro, 1900 m, *Woodson & Schery 695* (MO, US).

7. **Gonolobus edulis** Hemsl., Biol. Cent. Amer. Bot. 2: 331. 1882. TYPE: Costa Rica, San José, *Endres 213* (K, not seen).—FIG. 16C.

Vincetoxicum edule (Hemsl.) Standl., Contr. U. S. Natl. Herb. 23: 1680. 1926.
Gonolobus monnicheanus Woodson, Ann. Missouri Bot. Gard. 26: 303, *fig.* 2. 1939. TYPE: Panama, *Woodson et al. 1108* (MO).

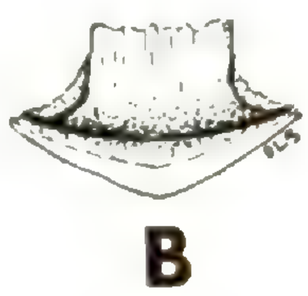
Herbaceous or subligneous *vines*; stems pilose when young, becoming glabrate with age. *Leaves* lanceolate to narrowly ovate, long acuminate apically, deeply cordate basally, puberulent on both surfaces, mostly 4–9 cm long and 2–4 cm wide; petioles pilose, 2–4 cm long. *Inflorescences* racemiform, mostly 5–10-flowered, puberulent and sparsely pilose; peduncles 1–4 cm long; pedicels 2–3 cm long. *Flowers* with the calyx pubescent outside, glabrous within, the lobes lanceolate, 5–8 mm long and 4–6 mm wide; corolla rotate, green, 1.7–2.7 cm in diameter, puberulent outside, barbellate within, especially at the base of the lobes, the lobes lanceolate-ovate to ovate, 7–10 mm long and 4–6 mm wide, the faucal annulus a low 5-angled ridge of tissue, ciliate but the cilia hidden by the barbellate hairs of the corolla limb; corona fleshy, thin, 5-lobed, the lobes smooth, apically rounded to broadly angular; the anther appendages when expanded are rounded apically, drying to truncate, ca. 0.9 mm long and 1.5 mm wide; gynostegium pentagonal; stigma head slightly depressed. *Follicles* said to be fusiform, smooth with 5 longitudinal wings, 10–12 cm long, 5 cm in diameter.

Now known from Costa Rica and Panama, this taxon is distinguished from other Panamanian taxa by the densely barbellate corolla.

CHIRIQUÍ: Near Boquete, *Allen 4661* (MO, US); *D'Arcy & D'Arcy 6504* (MO); *Davidson 800* (F, MO); *Luetyn 1520* (DUKE). Ca. 5.4 km del Hato de Volcán en la camino a Las Lagunas, *Correa & Lazor 1463* (MO). 2 mi. N of El Hato de Volcán, *Croat 10643* (MO). Between Boquete and Cerro Horqueta, *Duke 13707A* (DUKE, MO). Nueva California, *Tyson 5697* (DUKE, FSU, MO). Finca Lerida to Boquete, *Woodson et al. 1108* (MO).

8. **Gonolobus lewisii** L. O. Wms., Ann. Missouri Bot. Gard. 55: 49. 1968. TYPE: Panama, *Lewis et al. 2248* (F, holotype; DUKE, MO, isotypes).—FIG. 15.

Herbaceous *vines*; stems slender, densely soft pubescent when young, pilose in lines when older. *Leaves* ovate to elliptic, apically acuminate, basally cordate, strigose on both surfaces, 4–8 cm long and 2–4 cm wide; petioles sparsely strigose, mostly 2–4 cm long. *Inflorescences* umbelliform racemes, 10–15-flowered; peduncles puberulent, 2–3 cm long; pedicels sparsely pilose, 1.5–2.5 cm long. *Flowers* with the calyx sparsely strigose outside, glabrous within, the lobes lanceolate, 5–7 mm long and 2–2.5 mm wide; corolla rotate, 2.5–3 cm in diameter, green, glabrous throughout except for the annulus, the lobes lanceolate-ovate, 8–12 mm long and 4–7 mm wide, the faucal annulus a prominent thin ridge, ca. 0.5 mm high, annular, densely long ciliate; anther appendages fleshy, ca. 2.5 mm wide, with prominent lateral lobes which are usually twisted ribbon-like to project out from the anther ca. 0.8 mm, the entire surface densely and minutely papillate; the corona thin, fleshy, 5-lobed, lobes basically subquadrate but the



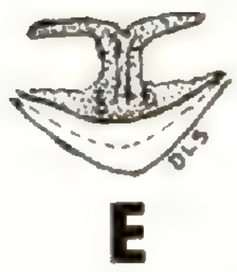


FIGURE 16. Representative anther appendages of species of *Gonolobus*. All × 7 unless otherwise indicated.—A. *G. albomarginatus* (Pittier) Woodson.—B. *G. allenii* Woodson.—C. *G. edulis* Hemsl.—D. *G. fuscoviolaceus* Woodson (× 14).—E. *G. ophioglossa* Woodson.—F. *G. inaequalis* L. O. Wms.

margins revolute to give a tapering appearance, extending beyond the annulus; gynostegium pentagonal; the stigma head depressed. *Follicles* unknown.

Now known only from Panama, the species is distinguished by the laterally lobed anther appendages: In one collection, *William 761*, the lobes of the appendages have failed to twist to a projecting position and instead project downward under the head of the gynostegium. The two Los Santos collections seen were collected on the same day by the same collecting party.

LOS SANTOS: Loma Prieta, Cerro Grande, *Duke 11888* (MO, OS); *Lewis et al. 2248* (DUKE, F, MO). DARIÉN: Cana and vicinity, *R. S. Williams 761* (NY, US).

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FLORA OF PANAMA[1]

BY ROBERT E. WOODSON, JR. AND ROBERT W. SCHERY
AND COLLABORATORS

Part IX

FAMILY 164. CONVOLVULACEAE[2]

DANIEL F. AUSTIN[3]

Herbs, *vines*, lianas, shrubs, or trees, the sap milky in some species; the rootstocks sometimes large; sometimes parasitic. *Leaves* mostly simple, pinnately lobed or pectinate, palmately compound in some species, or reduced to scales in *Cuscuta*; exstipulate. *Inflorescences* axillary, dichasial, solitary, racemose, or paniculate. *Flowers* perfect or imperfect (some African species), regular or slightly zygomorphic, small and inconspicuous to large and showy but mostly evanescent; sepals 5, free, imbricate, equal or unequal, persistent, occasionally accrescent in fruit; corolla sympetalous, tubular, funnelform, campanulate, urceolate or salverform, the limb with 5 lobes or teeth or almost entire, and with plicae and interplicae, the buds mostly induplicate; stamens 5, distinct, the filaments inserted on the corolla tube base alternate with corolla lobes, the anthers mostly linear or oblong, 2-celled, extrorse; disc annular or cupuliform, sometimes 5-lobed, occasionally absent; ovary superior, of 2 to 4 carpels, usually 2- or 3-locular, each locule biovulate, rarely 4- or 6-loculate or unilocular with 4 ovules, the style filiform, simple or bifid or 2 distinct styles present, the stigma capitate or bilobate or the stigmas 2 and linear, ellipsoid or globose. *Fruits* 1- to 4-locular, capsular, dehiscent by valves, transversely dehiscent, irregularly dehiscent or indehiscent; seeds 1–4, commonly fewer than ovules, glabrous or pubescent, the endosperm absent or scanty, cartilaginous, the cotyledons mostly foliaceous.

This worldwide family has numerous species in the tropics, fewer in temperate zones; it contains 40 or 50 genera, and 1200 or more species. The type genus is *Convolvulus* L. There is little agreement on generic delimitation, the family being largely natural. Three families have been segregated, however. The monotypic Humbertiaceae was segregated by Pichon (1951), but studies of other primitive elements in the family suggest that it is best included in the Convolvulaceae (Austin, 1973*a*). The Dichondraceae is apparently a sequential evolutionary phylad most closely allied with the tribe Poraneae, and it is also

---

[1] Assisted by National Science Foundation Grant No. GB-36202X (Thomas B. Croat, principal investigator).

[2] The late L. H. Shinners (1918–1971) began preparation of this manuscript and annotated many specimens cited here. His assistance in many aspects of work on the Convolvulaceae in Panama and elsewhere is gratefully acknowledged.

[3] Department of Biological Sciences, Florida Atlantic University, Boca Raton, Florida 33432.

ANN. MISSOURI BOT. GARD. 62: 157–224. 1975.

best included in the Convolvulaceae. The Cuscutaceae, apparently derived from the Dichondraceae or a common ancestor, has many unique characteristics, and most modern angiosperm phylogenists recognize it as a separate family. While there is considerable justification for this separation, its closest allies lie within the Convolvulaceae and the genus will be included for this treatment.

Several members of the family are of economic value. *Ipomoea batatas*, the sweet potato, is an important food plant throughout the world. Of lesser economic importance are the species cultivated for their flowers, *e.g. Argyreia nervosa* (Burm. f.) Boj., *Ipomoea* (*Calonyction*) *alba* L., *Ipomoea carnea* Jacq., *Ipomoea* (*Quamoclit pennata* (Desr.) Boj.) *quamoclit* L., *Ipomoea tricolor* Cav., *Porana paniculata* Roxb., and *Stictocardia campanulata* (L.) Merrill.

Pollen characteristics have classically been used as important criteria for generic delimitation in the family. It is difficult or impossible to distinguish *Merremia*, *Operculina*, and *Ipomoea* without resorting to pollen. The first two genera have smooth pollen; *Ipomoea* has spinulose grains. The differences are fairly easily seen with a dissecting microscope. This obscure pollen characteristic and the necessity for fruiting material to separate *Merremia* and *Operculina* led Shinners (1970) to lump these into *Ipomoea* in his last publication on the Convolvulaceae before his untimely death.

Hallier (1893) divided the family by using pollen characteristics as major criteria. While there is no doubt that pollen is an important criterion for understanding phyletic relationships, there is no reason why it should be weighted in such a heavy manner. Present knowledge of the family suggests re-examination of Hallier's tribal arrangements. I have discussed this elsewhere (Austin 1973a) and will basically follow my previous tribal arrangement. The following synoptic key indicates tribal separations. The artificial key should be used to identify Panamanian plants.

Literature:

Austin, D. F. The American Erycibeae (Convolvulaceae); *Maripa, Dicranostyles*, and *Lysiostyles*—I. Systematics. Ann. Missouri Bot. Gard. 60: 306–412. 1973*a* [1974].

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Hallier, H. Versuch einer natürlichen Gliederung der Convolvulaceen auf morphologischer und anatomischer Grundlage. Bot. Jahrb. (Syst.) 16: 453–591. 1893.

Pichon, M. Le fruit et la graine des Humbertiacées. Bull. Soc. Bot. France 98: 235–237. 1951.

Shinners, L. H. Convolvulaceae. Pp. 1241–1261, *in* D. S. Correll & M. C. Johnston, "Manual of the Vascular plants of Texas." 1970.

Verdcourt, B. Convolvulaceae. *In* C. E. Hubbard & E. Milne-Redhead, "Flora of Tropical East Africa." 1963.

SYNOPTIC KEY TO TRIBES

a. Leaves absent or scale-like; plants without chlorophyll and usually yellowish or orange; styles usually 2 and distinct, occasionally connate basally; fruits capsular, opening either

by circumscissile dehiscence or irregularly; cotyledons absent ..... Tribe 8. Cuscuteae (*Cuscuta*)

aa. Leaves present and fully formed although variable; plants with chlorophyll; styles mostly 1 or rarely 2, distinct or connate basally; fruits capsular and dehiscent or baccate or nut-like; cotyledons present.

b. Prostrate herbs, to 1 m long; flowers mostly solitary in leaf axils; calyx connate basally, deeply 5-lobed; fruits deeply 2-lobed or almost 2 and separate, utriculate ..... Tribe 7. Dichondreae (*Dichondra*)

bb. Twining, diffuse, or erect vines, herbs or lianas, mostly over 1 m long if twining, usually smaller if erect or diffuse (prostrate in *Evolvulus nummularius*); flowers solitary to paniculate; calyx lobes free; fruits entire, capsular to operculate or indehiscent.

c. Fruits indehiscent, nut-like to baccate; large lianas and woody vines; flowers white, lavender to scarlet.

d. Leaves elliptic, coriaceous to chartaceous, glabrous to glabrate; flowers campanulate-funnnelform, lavender to white-lavender; fruits nut-like; embryos with non-plicate fleshy cotyledons ..... Tribe 1. Erycibeae (*Maripa*)

dd. Leaves ovate-cordate, chartaceous to membranaceous, glabrous to densely pubescent below; flowers mostly funnelform, rarely campanulate-funnelform, scarlet, lavender or white; fruits baccate and 4-seeded or chartaceous and 1-seeded; embryos with foliaceous plicate cotyledons ..... Tribe 6. Argyreieae (*Argyreia, Stictocardia, Turbina*)

cc. Fruits dehiscent, capsular to operculate (indehiscent in *Iseia*); twining vines, suffrutescent shrubs, herbs or woody vines; flowers white, yellow, orange, pink, red or lavender.

e. Flowers mostly smaller than 2 cm across, broadly campanulate to subrotate, white or blue; small vines or diffuse to suberect suffrutescent herbs, mostly herbaceous ..... Tribe 3. Convolvuleae (*Evolvulus, Jacquemontia*)

ee. Flowers mostly larger than 2 cm across, broadly campanulate, funnelform or salverform, white, yellow, orange, pink, red or lavender; medium to large vines, herbaceous to woody, rarely large erect to scrambling shrubs.

f. Corolla interplicae densely pubescent, corollas white, funnelform to subcampanulate; styles bipartite or 2 (one in *Iseia*); fruits capsular (*Bonamia*) or indehiscent (*Iseia*) ..... Tribe 2. Cresseae (*Bonamia, Iseia*)

ff. Corolla interplicae glabrous or with inconspicuous indument, corollas mostly colored, sometimes white, campanulate, funnelform or salverform; style one; fruits capsular to operculate.

g. Corollas yellow or white and campanulate, if pink then salverform; stamens often spirally twisted at anthesis; pollen 3-colpate or pantocolpate ..... Tribe 4. "Merremioids" (*Aniseia, Merremia, Operculina*)

gg. Corollas red, orange, pink, lavender or purple, if white then salverform, mostly funnnelform or salverform; stamens rarely spirally twisted at anthesis, usually straight; pollen pantoporate and spinulose ..... Tribe 5. Ipomoeeae (*Ipomoea*)

Artificial Key to Genera

a. Plants parasitic; stems yellow to orange, without chlorophyll; leaves reduced to scales ..... 14. *Cuscuta*

aa. Plants not parasitic; stems green or brownish, chlorophyllous; leaves normally developed.

b. Flowers to 5 mm across; ovary and fruit deeply biolobate or carpels distinct; leaves reniform; small repent herbs ..... 13. *Dichondra*

bb. Flowers more than 5 mm across; ovary and fruit entire; leaves various, rarely reniform; if repent herbs, not small.

c. Fruits indehiscent, subbaccate to dry.

d. Leaves basally cordate to subcordate.

e. Sepals enveloping the fruit; flowers scarlet ..... 11. *Stictocardia*

ee. Sepals reflexed in fruit; flowers white or purple.

f. Corolla white or lavender, often dark inside at base; fruits with enlarged sepals, dry; seeds mostly one, glabrous to puberulent .. 12. *Turbina*

ff. Corolla purple, darker inside; fruits without enlarged sepals, subbaccate; seeds 1–4, glabrous ..... 10. *Argyreia*
dd. Leaves basally obtuse to acute.
g. Corolla white; fruits bilocular with spongy mesocarp; seeds 4, perisperm absent; herbaceous vines ..... 3. *Iseia*
gg. Corolla lavender to purple; fruits incompletely bilocular without mesocarp; seeds 1(–4), perisperm present; woody lianas ..... 1. *Maripa*
cc. Fruits dehiscent, dry; mostly herbs, less commonly woody vines.
h. Style one and bifid, or styles 2 and distinct.
i. Lianas; style one, bifid; stigmas capitate ..... 2. *Bonamia*
ii. Herbs or small suffrutescent shrubs, not scandent; styles 2; stigmas elongate, bifid ..... 5. *Evolvulus*
hh. Style one, entire.
j. Sepals unequal, the outer larger and concealing the inner ..... 8. *Aniseia*
jj. Sepals equal to subequal.
k. Stigmas ellipsoid to oblong ..... 4. *Jacquemontia*
kk. Stigmas globose to bi-globose.
l. Pollen smooth; 3-colpate to polycolpate.
m. Capsule transversely dehiscent ..... 7. *Operculina*
mm. Capsule longitudinally or irregularly dehiscent ..... 6. *Merremia*
ll. Pollen spinulose; pantoporate ..... 9. *Ipomoea*

1. ERYCIBEAE

Erycibeae (Endl.) Hall. f., Bot. Jahrb. (Syst.) 16: 576. 1893. TYPE: *Erycibe* Roxb.

Maripeae Webb & Berth., Hist. Nat. Îles Canaries, Bot. 3,2(3): 27. 1844. TYPE: *Maripa* Aubl.
Dicranostyleae Meisn. *in* Mart., Fl. Bras. 7: 205. 1869. TYPE: *Dicranostyles* Benth.
Convolvuloideae-Dicranostyleae Peter *in* Engl. & Prantl, Nat. Pfl. 4(3a): 14–18. 1891.
Convolvuloideae-Convolvuleae-Argyreiinae Peter *in* Engl. & Prantl, Nat. Pfl. 4(3a): 20–22, pro parte. 1891.
Convolvuloideae-Erycibeae Peter *in* Engl. & Prantl, Nat. Pfl. 4(3a): 36–37. 1891.
Erycibinae (Endl.) Ooststr. *in* Steenis, Fl. Malas. 4: 389. 1935.
Dicranostylinae (Meisn.) Ooststr. *in* Steenis, Fl. Malas. 4: 389. 1935.

1. MARIPA

Maripa Aubl., Hist. Pl. Guiane Fr. 1: 230, *t. 90*. 1775. TYPE: *Maripa scandens* Aubl.

Mouroucoa Aubl., Hist. Pl. Guiane Fr. 1: 142, *t. 54*. 1775. TYPE: *M. violacea* Aubl. = *Maripa violacea* (Aubl.) Oostr. *in* Lanjouw & Uittien.

Lianas reaching over 30 m; larger stems fluted, to 30 cm in diameter, the younger stems often angled. *Leaves* simple, mostly elliptical, ovate or obovate to oblong, glabrous or occasionally stellate. *Inflorescences* of panicles terminal on lateral branches, sometimes racemose. *Flowers* often fragrant; sepals 5, equal to subequal, ovate to rotund, the inner often emarginate, the outer acute to rounded, mostly coriaceous with membranaceous margins, ciliate, glabrous or pubescent; corolla funnelform to campanulate, white to violet or pinkish, the lobes mostly shallow, rounded or acute, pubescent on the interplicae; stamens usually included, the filaments triangular-dilate, glandular-pubescent, filiform above, the anthers subsagittate to sagittate, narrowly ovate, the pollen 3-colpate or pantocolpate; ovary incompletely bilocular with a partial septum in lower portion, mostly glabrous, occasionally pubescent apically, the style entire, rarely

divided for ½ the length or less, the stigma capitate, bilobate, the lobes free or closely appressed and the style entire. *Fruits* nut-like, rounded to ellipsoid, the pericarp ligneous, firm to hard; seeds 1–4 through abortion, glabrous, ovoid to oblong-ellipsoid, rounded, flattened or trigonous if more than one per fruit.

An American genus of 19 species. Most of the species occur in northern South America. Two closely allied species are found in Panama.

Literature:

Austin D. F. The American Erycibeae (Convolvulaceae): *Maripa*, *Dicranostyles* and *Lysiostyles*—I. Systematics. Ann. Missouri Bot. Gard. 60: 306–412. 1973a [1974].

———. The American Erycibeae (Convolvulaceae). *Maripa*, *Dicranostyles*, and *Lysiostyles*—II. Palynology. Pollen & Spores 15: 203–226. 1973.

a. Leaves chartaceous to subcoriaceous, reticulate beneath, veins prominent beneath; flowers densely sericeous outside; fruits smooth to slightly striate when dry ..... 1. *M. nicaraguensis*

aa. Leaves thick coriaceous, rugose beneath, veins not prominent beneath; flowers tomentose outside; fruits strongly striate when dry ..... 2. *M. panamensis*

1. **Maripa nicaraguensis** Hemsl., Biol. Centr. Amer. Bot. 2: 382. 1882. TYPE: Nicaragua, *Tate 418* (K, holotype).

Murucoa nicaraguensis (Hemsl.) O. Kuntze, Rev. Gen. Pl. 2: 446. 1893.

Maripa colombiana Gleason, Bull. Torrey Bot. Club 56: 110. 1929. TYPE: Colombia, near Salento, *Andre 2355* (K, holotype).

M. cuatrecasasii Moldenke, Phytologia 2: 139. 1946. TYPE: Colombia, El Valle, Río Calima, *Cuatrecasas 16531* (NY, holotype).

Lianas; stems smooth to slightly angled, grayish-brown to brown. *Leaves* elliptic to lanceolate, 9–15(–25) cm long, the base obtuse to rounded, the apex acute to shortly acuminate, chartaceous to subcoriaceous, glabrescent. *Inflorescences* terminal, paniculate-thyrsiform with reddish peltate glandular trichomes on the branches; bracts triangular to triangular-ovate, to 2 mm long, mostly persistent in flower, caducous in fruit. *Flowers* with pedicels 4–8(–12) mm long; sepals ovate to broadly ovate, 7–8 mm long, coriaceous to membranaceous, ciliate, the exterior lobes with reddish glandular basal trichomes, the interior lobes glabrous to appressed-pubescent outside; corolla lilac to pinkish, the tube base nearly white (living), 30–45 mm long. *Fruits* ellipsoid, broadly ellipsoid to suborbicular, 20–30 mm in diameter, the surface smooth to reticulate, yellow and turning brown to dark brown; seeds ovoid, 20–22 mm long, 11–13 mm in diameter.

This species flowers from January to August and fruits from April to January. It ranges through Belize, Guatemala, Nicaragua, Costa Rica, Panama, Colombia and Ecuador (Esmeraldas).

Maripa nicaraguensis and *M. panamensis* may be distinguished by leaf texture and venation and by the dried fruits. The mature leaves of *M. nicaraguensis* are invariably chartaceous and reticulate below with prominent veins. *Maripa panamensis* has coriaceous leaves with the veins sunken and obscured in the

rugose lower surface. Both species have smooth fruits when immature, but *M. panamensis* produces strongly striate fruits at maturity.

BOCAS DEL TORO: Río Teribé, between Quebrada Tregalo and Puerto Palenque, *Kirkbride & Duke 526* (MO). CANAL ZONE: Natural bridge, SE edge of Madden Lake, *Gentry 5606* (MO). 12 mi. S of Colón, *Tyson, Dwyer & Blum 4477* (MO). COCLÉ: El Valle, *Duke 13183* (MO). COLÓN: Santa Rita lumber road, ca. 15 km E of Colón, *Dressler 3406* (MO). DARIÉN: Between Quebrada Venado and Peje Swamp on headquarters of Río Tuqueza, *Bristan 1017* (MO). Río Ucurgantí, *Bristan 1141* (MO). Río Chucunaque, between Río Membrillo and Río Subcutí, *Duke 8608* (MO). Road from El Real to Pinogana, *Duke 4898* (MO). Perrecenico River, *Duke & Dristan 237* (MO). Río Arretí, *Duke & Nickerson 14913* (MO); *Duke 8356* (MO). Near Campamento Buena Vista, Río Chucunaque above confluence with Río Tuquesa, *Stern et al. 867* (G, GH, MO, US). Cana-Quasi trail, Chepigana, *Terry & Terry 1614* (A, F, MO). Near Marragantí, *Williams 985* (NY).

2. **Maripa panamensis** Hemsl., Biol. Centr. Amer. Bot. 2: 382. 1882. TYPE: Panama, *Fendler 255* (K, holotype; GH, MO, US, isotypes).—FIG. 1.

Murucoa panamensis (Hemsl.) O. Kuntze, Rev. Gen. Pl. 2: 446. 1893.

Lianas; stems terete, angled, light brown. *Leaves* ovate, elliptic to obovate, 7–15 cm long, the base cuneate to ± rounded, the apex shortly acuminate to obtuse, coriaceous, with an obvious raised, rugose pattern below between the secondary veins, dull above, glabrescent. *Inflorescences* terminal, paniculate-thyrsiform, covered with reddish glandular trichomes; bracts triangular, caducous, densely covered with peltate glandular trichomes. *Flowers* with the pedicels 3–4 mm long; sepals ovate to broadly ovate, 7–8 mm long, coriaceous, the external lobes with reddish peltate glandular trichomes, the inner with appressed trichomes or glabrous; corolla violet to pale lilac, 25–30(–37) mm long. *Fruits* ellipsoid to broadly ellipsoid, 17–25 mm in diameter, sulcate with 16–22 sulcae when dry, yellow turning light to dark brown; seeds ellipsoid to ovoid, 15–17 mm long, 9–10 mm in diameter.

This species flowers from December to April and fruits from April to September. It occurs in eastern Panama, northern Colombia, and northern Venezuela.

CANAL ZONE: Near mouth of Río Chagres, *Allen 890* (G, MO). Barro Colorado Island, *Aviles 885* (F); *Bailey & Bailey 82* (F), *640* (GH); *Bangham 411* (A); *Croat 8743* (MO); *Dwyer 1477* (MO); *Frost 211* (F); *Kenover 504* (US). Road between Locks and Ft. Sherman, *Croat 15363* (MO). Between Ft. Sherman and Ft. San Lorenzo, *Croat 15428* (MO). Chagres, *Fendler 255* (GH, K, MO, US). Bojio Station, *Hayes 140* (BM, K). Las Cascadas, *Johansen 21* (US). W of Limón Bay road along Río Piña—Río Media divide, *Johnston 1602* (A). W of Limón Bay, Charity Peaks, *Johnston 1524* (A, MO). Tortuguilla Point, *Johnston 1816* (MO). Pipeline road between mile markers 0 and 11.1, ca. 16 mi. N of Gamboa, *Lewis et al. 5467* (MO); *Lindsay 467* (F). Río Agua Salud, near Frijoles, *Piper 5849* (BM, US). Near Frijoles, *Piper 5796* (US). Agua Clara, on Trinidad River, *Pittier 3994* (NY, US). Barro Colorado Island, *Salvoza 876* (A); *Shattuck 772* (F, MO), *885* (MO, US); *Standley 40979* (US); Wheeler Trail, *Starry 138* (MO). Gamboa, Navy Pipeline road, 10 mi. NE of Gamboa Bridge, *Stern & Chambers 20* (MO). Between Tumba Vieja and Salamanca, *Steyermark & Allen 16756* (M). Fort Sherman, *Tyson 3760* (MO). Road from Fort Sherman to Fort San Lorenzo, *Tyson & Blum 3760* (MO). Barro Colorado Island, *Wetmore & Woodworth 855-10, 880-39, 886-47, 898-59* (all A, F); *Wilson 63* (F, MO); *Woodworth & Vestal 418* (A, F, M), *503* (F, MO). COLÓN: Near Camp Pina, *Allen 3428* (BR, F, G, GH, MO, NY, U, US). Santa Rita lumber road, ca. 15 mi. E of Colón, *Dressler 3406* (MO). Santa Rita Ridge, 2 mi. from Transisthmian Highway, *Gentry 1438* (MO). 10 mi. SW of Portobelo, *Liesner 1094* (MO). Road to Piña, *Kirkbride & Hayden 323* (MO). DARIÉN: Camp Eslo-

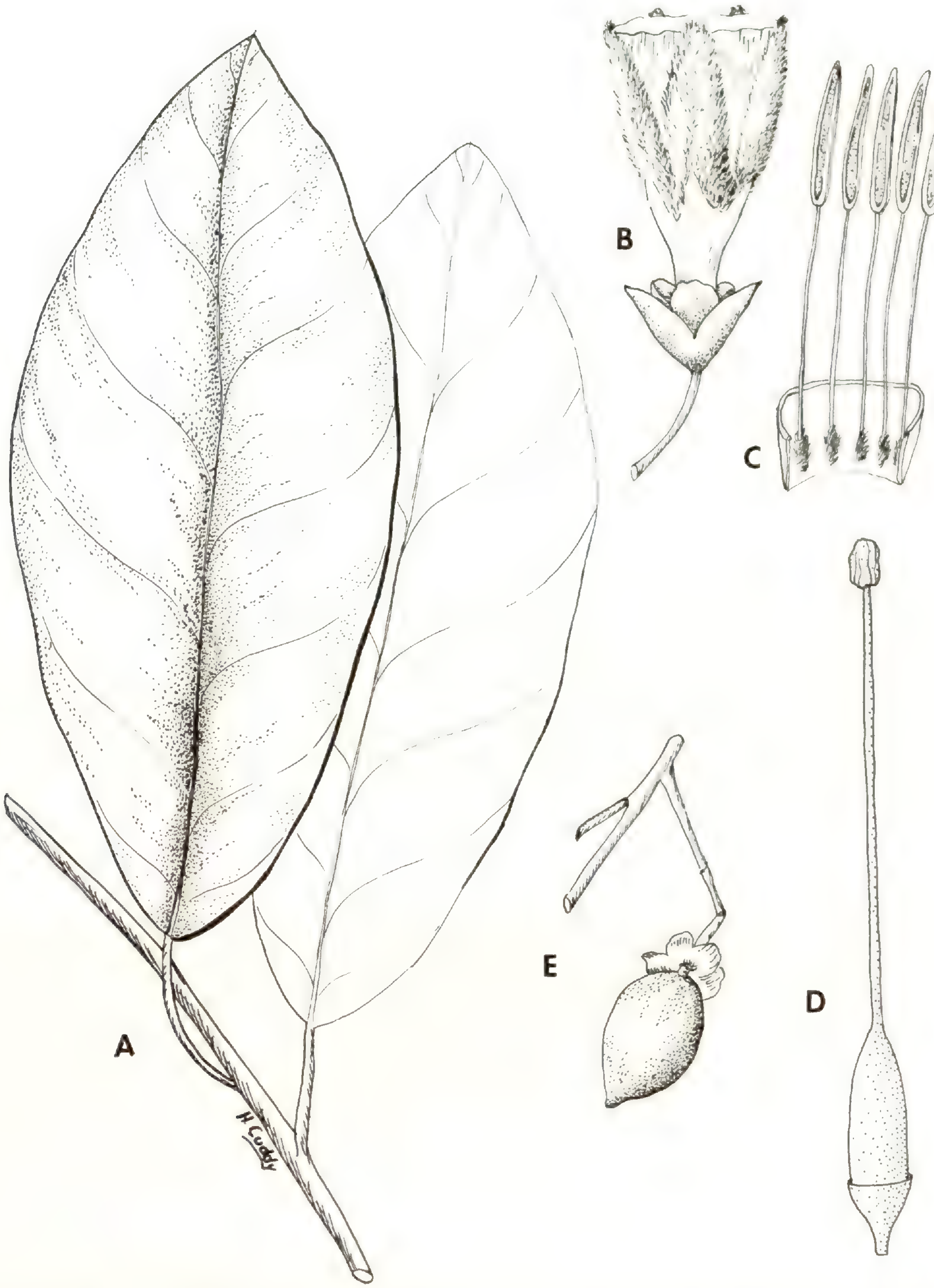

FIGURE 1. *Maripa panamensis* Hemsl.—A. Stem with leaves (× 7/10).—B. Flower, external view (× 1⅖).—C. Dissection of corolla with stamens and filament attachment (× 2⅘).—D. Gynoecium (× 4⅘).—E. Fruit (× 7/10).

ganti, *Duke 15503* (MO). Cerro Pidiaque, *Duke 8076, 8122, 8123* (all MO). Hydro Camp Pico Pendejo on Río Sabana, *Duke 15431* (MO). Cocalito near beach, *Dwyer 5135* (MO). Near La Palma, *Pittier 5489* (GH, NY, US). Near Cana, *Stern et al. 510* (G, MO, US). Cerro Pidiaque, *Tyson, Duke & Loftin 3833* (MO). 3 mi E. of Santa Fé, *Tyson et al. 4717* (MO). Marragantí, *Williams 985* (US). PANAMÁ: Along Río Juan Díaz, *Allen 935* (G, GH,

MO). Hills above Campana, *Allen 1695* (MO). Along PanAm highway, ca. halfway between El Llano and Río Mamoní, *Duke 5650* (MO). Cermeño, *Dwyer & Robyns 104* (MO). Cladonia Harbor, Mt. Vernon, *Elmore L13* (GH). Trail behind Peluca meterological station, *Kennedy & Dressler 2977* (MO). Road from El Llano to Carti-Tupile in San Blas, *Liesner 1229* (MO). Near Arraijan, *Woodson et al. 1338* (A, F, MO, NY). SAN BLAS: Road between Mandinga and Cangandi, *Duke 14731* (MO).

2. CRESSEAE

Cresseae Benth. & Hook., Gen. Pl. 2: 868. 1873. TYPE: *Cressa* L.

Dicranostyleae sensu Hall. f., Bot. Jahrb. (Syst.) 16: 569. 1893, excl. *Dicranostyles* Benth.
Cresseae Roberty, Candollea 14: 28. 1952, nom. illeg. *Dicranostylinae* sensu Ooststr., Fl. Males. 4: 389. 1953.

The circumscription of this tribe was recently amended (Austin 1973a).

2. BONAMIA

Bonamia Thouars, Hist. Vég. Îsl. France 1: 33. 1804, nom. cons. TYPE: *B. madagascariensis* Poir.

Breweria R. Br., Prodr. 487. 1810. TYPE: *Bonamia linearis* (R.Br.) Hall. f.
Trichantha Karst. & Triana, Linnaea 28: 437. 1856, non Hook. (1844). TYPE: *T. ferruginea* Karst. & Triana = *Bonamia trichantha* (Karst. & Triana) Hall. f.

Lianas to small scrambling shrubs or herbaceous vines, mostly perennial, glabrous to pubescent. *Leaves* entire, lanceolate to ovate. *Inflorescences* of solitary flowers or few-flowered dichasia or panicles; the bracts small. *Flowers* with the sepals obtuse to acute, subequal, the outer ones larger and suborbicular; corolla campanulate or funnelform, the limb plicate, the interplicae ferrugineous; stamens included, the filaments filiform, mostly triangular-dilate and glandular-pubescent at the base, the anthers oval or oblong, the pollen 3-colpate; ovary 2-locular, 4-ovulate, the style filiform, bifid to almost entire, or the styles 2 and free, the stigmas capitate, subglobose. *Fruits* capsular, 4-valvate, pericarp membranaceous to coriaceous; seeds 4 or fewer by abortion, glabrous or pubescent.

There are about 45 species of this genus in the tropics and subtropics of both hemispheres. Two species occur in Panama. Myint and Ward (1968) report a third species for Central America, but this species belongs to the genus *Itzaea* (Austin, 1971).

Literature:

Austin, D. F. Relations of *Itzaea sericea*. Biotropica 3: 32–35. 1971.

Myint, T. & D. B. Ward. A taxonomic revision of the genus *Bonamia* (Convolvulaceae). Phytologia 17: 121–239. 1968.

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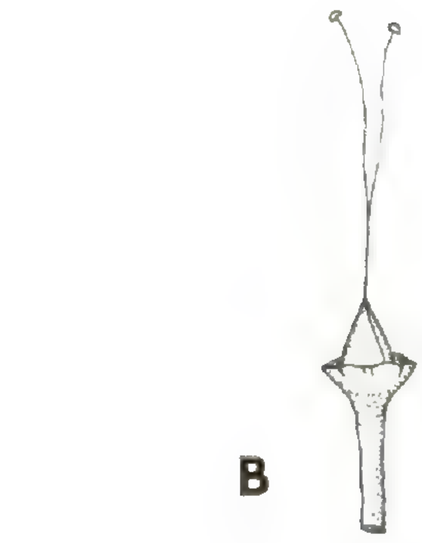
FIGURE 2. *Bonamia trichantha* (Karst. & Triana) Hall. f.—A. Habit (× ½).—B. Gynoecium (× 1½).—C. Androecium (× 2½).—D. Seed showing comose trichomes (× 1).—E. Fruits (× ½). [A after *Standley 27970* (US). B–C after *Tyson et al. 3121* (MO). D after *Blum 2227* (MO). E after *Dwyer et al. 7317* (MO).]



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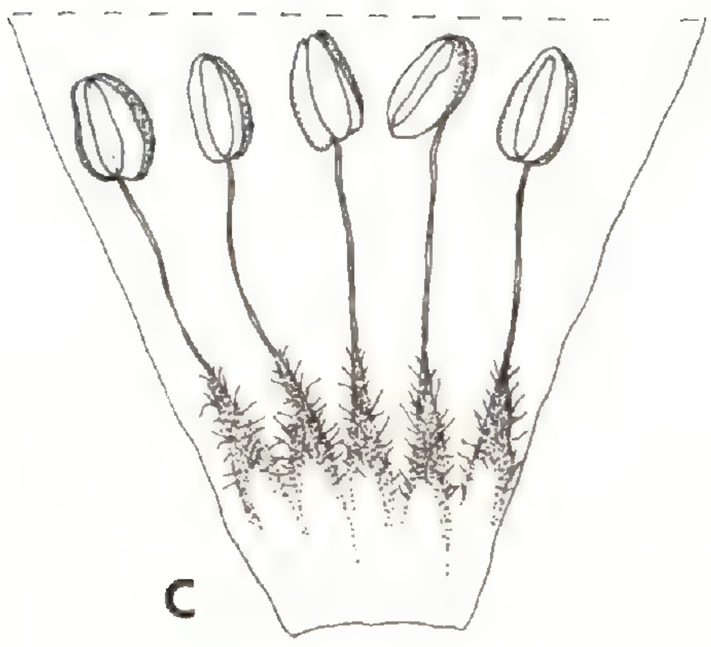

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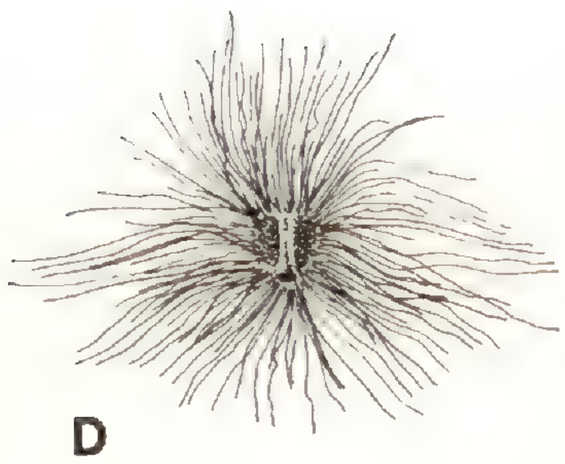


D

E

A

a. Leaves sparsely pubescent, glabrous or glabrescent on both sides; inner and outer sepals sparsely pubescent to glabrous, to 5 mm long; seeds pubescent with long yellowish trichomes ..... 2. *B. trichantha*
aa. Leaves densely pubescent on both sides; inner and outer sepals densely pubescent, to 10 mm long; seeds glabrous ..... 1. *B. sulphurea*

1. **Bonamia sulphurea** (Brandeg.) Myint & Ward, Phytologia 17: 178. 1968.

Breweria sulphurea Brandeg., Univ. California Publ. Bot. 4: 384. 1913. TYPE: Mexico, Vera Cruz, *Purpus 5995* (US, holotype).

Lianas; stems covered with short brownish or yellowish ascending, appressed trichomes, glabrescent. *Leaves* coriaceous, elliptic-oblong to oval, 4–7.5 cm long, apically rounded, muricate, basally rounded, appressed pilose above, densely yellowish pilose to tomentose below. *Flowers* several in axillary compound cymes; sepals lanceolate-oblong to ovate-oblong, 1–1.5 cm long, acute, yellowish appressed-pilose; corolla white, 1.5–2 cm long, interplicae hirsute, styles 2, free to ovary apex, the 2 stigmas globose. *Fruits* capsular, subconical, apically hirsute; seeds ovate, black, glabrous.

This species flowers in December. It occurs in Mexico (Vera Cruz), Guatemala, Honduras, and Panama.

LOS SANTOS: Roadside near Las Tablas, *Burch et al. 1271* (GH, MO, NY, US).

2. **Bonamia trichantha** (Karst. & Triana) Hall. f., Bot. Jahrb. (Syst.) 16: 528. 1893. TYPE: Based on *Trichantha ferruginea* Karst & Triana.—FIG. 2.

Trichantha ferruginea Karst. & Triana, Linnaea 28: 438. 1856. TYPE: Colombia, Magdalena, *Triana 2146* (not seen).
Breweria mollis Pittier, Jour. Washington Acad. Sci. 17: 284. 1927. TYPE: Venezuela, Calvario de Guanare, *Pittier 12046* (not seen).
B. longipaniculata Pittier, Jour. Washington Acad. Sci. 17: 284. 1927. TYPE: Venezuela, Trujillo, *Pittier 10733* (not seen).
Maripa acuminata Rusby, Descr. New Sp. S. Amer. Pl. 102. 1920. TYPE: Colombia, Magdalena, *Smith 877* (NY, holotype; US, isotype).

Lianas; stems woody, perennial, tomentose when young, glabrescent. *Leaves* ovate, oblong to ovate-oblong, 5–12(–15) cm long, cordate to obtuse basally, acute, obtuse, attenuate to obtuse-mucronate apically, glabrous or less commonly sparsely pubescent above, tomentose to glabrate beneath. *Flowers* in axillary cymes or terminal thyrses, few- to many-flowered; sepals orbicular to orbicular-ovate, 5–7 mm long, the outer sepals ferrugineous to pubescent-glabrescent, the inner sepals sparsely pubescent to glabrate; corollas white, 1–2 cm long, interplicae hirsute; styles shortly connate basally, the stigmas 2, globose or capitate and commonly subbilobate. *Fruits* capsular, ovoid to subconical, 8–15 mm in diameter; seeds ovoid, brown, comose at least on the margins.

This species flowers from December to February. It occurs in Panama, Colombia and Venezuela.

CANAL ZONE: Near TTC Albrook Tower, *Blum 2227* (MO). U. S. Army Test Site, Albrook, *Dwyer & Robyns 121* (MO). DARIÉN: Río Mortí, *Duke 10167* (MO). Near Refugio, N of Santa Fé, *Duke 10287* (MO). Near Refugio, *Duke 10305* (MO). Near Punta Garachiné, *Duke 10473, 10498* (both MO). LOS SANTOS: Road from Tonosí to Guanico, *Tyson et al.*

3121 (MO). PANAMÁ: Cerro Jefe, *Dwyer et al. 7317* (MO). Taboga Island, *Standley 27970* (MO, US).

3. ISEIA

Iseia O'Donell, Bol. Soc. Argent. Bot. 5: 77. 1953. TYPE: *I. luxurians* (Moric.) O'Donell.

Vines with many branches, rooting at the nodes, the branches pubescent. *Leaves* petiolate, elliptic, oblong to lanceolate, basally cuneate to rounded, apically obtuse to acute, mucronate, pubescent to glabrescent. *Flowers* in 2–10-flowered cymes, occasionally solitary; sepals equal to subequal, the external ones elliptic to suborbicular, pubescent to glabrate, the internal ones glabrous or pubescent on a median line, ciliate; corolla funnelform, white, the interplicae with dense ferrugineous indument; stamens of 2 lengths, the filaments basally glandular-pubescent, the pollen 3-colpate; ovary ovoid, bilocular, 4-ovulate, basally glabrous, apically pubescent, the style filiform, the stigma bi-globose. *Fruits* indehiscent, subglobose, blackish, glabrous or the upper part pubescent, the mesocarp spongy, the endocarp crustaceous, woody, bilocular; seeds 4, dark, glabrous to winged with small marginal trichomes.

This monotypic American genus occurs from Honduras south to the northern part of Argentina. According to O'Donell the species is most common along river and stream margins; he attributes this to dispersal of the fruits by water, saying that they float for more than two months.

1. **Iseia luxurians** (Moric.) O'Donell, Bol. Soc. Argent. Bot. 5:77. 1953.—FIG. 3.

Ipomoea luxurians Moric., Pl. Nouv. Amer. 58, *t.* 39. 1839. TYPE: Brazil, Bahia, *Blanchet 2914* (not seen).
I. sericea Spreng. *ex* Choisy *in* DC., Prodr. 9: 368. 1845, non Blume (1825). TYPE: Santa Marta, Colombia, *Bertero* (not seen).
I. jamesonii Choisy *in* DC., Prodr. 9: 367. 1845. TYPE: Ecuador, Guayaquil, *Arnott & Jameson* (not seen).
I. sericantha Griseb., Fl. Brit. W. Ind. 471. 1861, non Miquel (1850). Nom. nov. *I. sericea* Choisy.
I. grisebachiana Meisn. *in* Mart., Fl. Bras. 7: 264. 1869. Nom nov. for *I. sericantha* Griseb.
Jacquemontia luxurians (Moric.) Hall. f., Bot. Jahrb. (Syst.) 16: 543. 1893.

Lianas; stems much branched, the branches rooting, retrorse-pubescent or tomentose with reddish trichomes, glabrescent. *Leaves* elliptic, oblong to lanceolate, 1.5–12 cm long and 0.5–4 cm wide, basally cuneate to rounded, apically obtuse to acute, mucronate, usually with appressed sericeous indument at least on major veins, glabrescent. *Flowers* in 1–10-flowered cymes, the cymes usually pubescent, pedicels 3–10 mm long; sepals elliptic to obovate, 7–12 mm long and 5–7 mm wide, obtuse to acute, mucronate, mostly pubescent, ciliate, the inner sepals often with only a central line of pubescence; corolla white, 3–4 cm long, funnelform, the interplicae densely villose; stamens unequal, the filaments basally glandular pubescent; style one, the stigma biglobose, ovary ovoid, basally glabrous, apically pubescent. *Fruits* indehiscent, subglobose, 9–14 mm in diameter, black, glabrous or pubescent above; seeds 4, dark, 4–6 mm long, glabrous to winged with marginal trichomes.

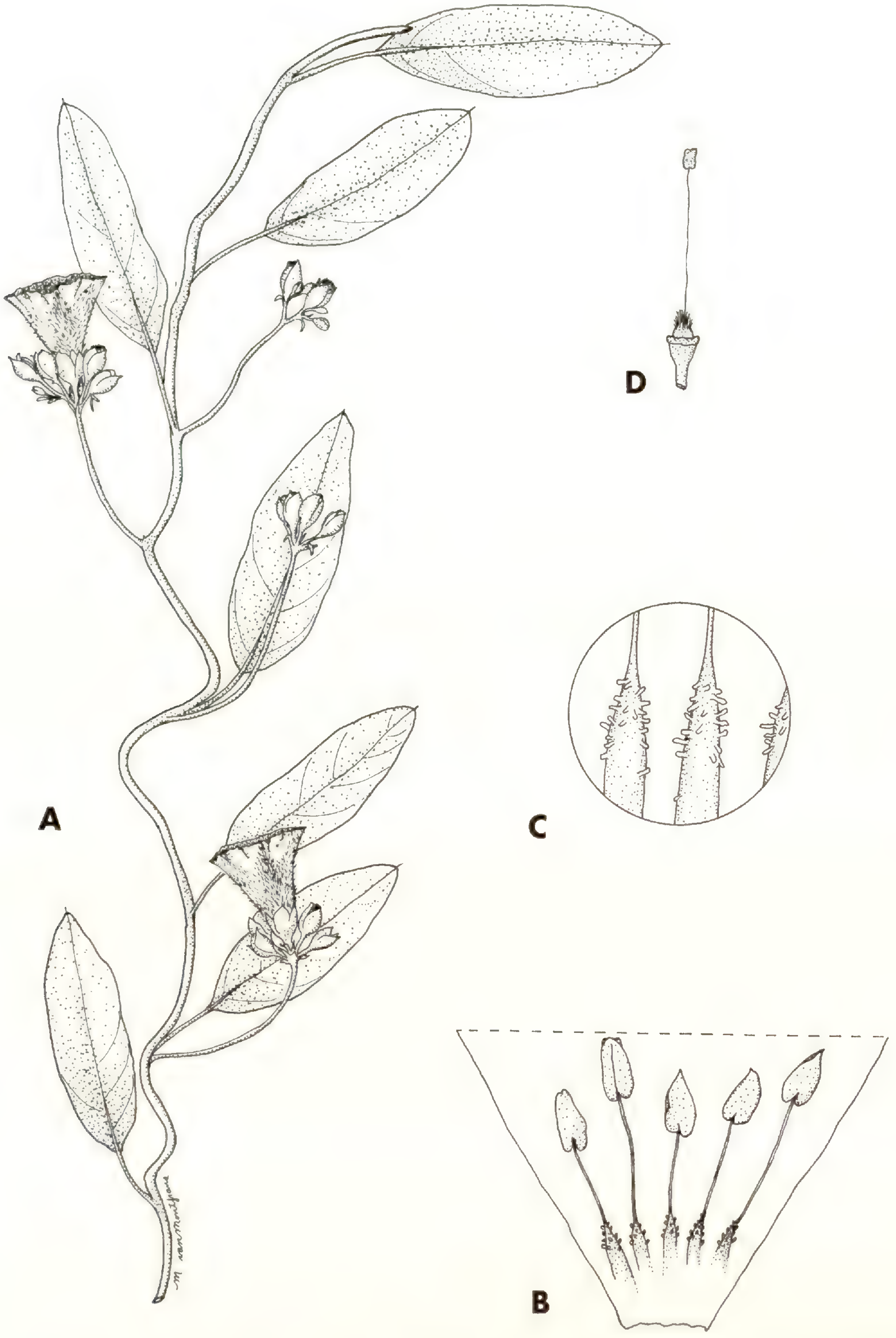


FIGURE 3. *Iseia luxurians* (Moric.) O'Donell.—A. Habit (× 3/5).—B. Corolla dissection (× 3).—C. Glandular trichomes at filament bases (× 6).—D. Gynoecium (× 1⅘). [A after *Burch et al. 1106* (MO). B–D after *Burch et al. 1353* (MO).]

This species flowers in December. It occurs in Honduras, Panama, Colombia, Venezuela, Trinidad and south to Argentina.

CANAL ZONE: Near Gamboa, Río Mandinga ca. 1 mi. up from the canal, *Kennedy et al.* 2385 (MO). Gamboa, Chagres River ca. ¼ mi. up from hyacinth control building, *Kennedy et al. s.n.* (MO). DARIÉN: Río Chico, *Burch et al. 1106* (GH, MO, US). HERRERA: Road from Chitré to Divisa, *Burch et al. 1353* (GH, MO, US). PANAMÁ: Near Chepo, *Hunter & Allen 98* (MO).

3. CONVOLVULEAE

Convolvuleae (Choisy) Choisy *in* DC., Prodr. 9: 325. 1845. TYPE: *Convolvulus* L.

Convolvuleae Choisy, Mém. Soc. Phys. Genève 6: 404. 1833, as "sectio."
Convolvuleae (Choisy) Endl., Enchir. Bot. 373. 1841, as "subordo."
Convolvulinae Meisn. *in* Mart., Fl. Bras. 7: 205. 1869.
Convolvuleae Baillon, Hist. Pl. 10: 321. 1891, as "série."

4. JACQUEMONTIA[4]

Jacquemontia Choisy, Mém. Soc. Phys. Genève 6: 476. 1833. LECTOTYPE: *Convolvulus pentanthus* Jacq. = *Jacquemontia pentantha* (Jacq.) G. Don.

Thyella Raf., Fl. Tell. 4: 84. 1838. LECTOTYPE: *T. tamnifolia* (L.) Raf. = *Jacquemontia tamnifolia* L.

Herbs or suffrutescent procumbent shrubs, glabrous or densely pubescent. *Leaves* petiolate, mostly cordate at the base, entire, dentate or lobate. *Flowers* axillary, solitary in scorpioid cymes or in umbelliform or head-like cymes; small or medium-sized; the bracts small and linear to lanceolate or large and foliose; sepals 5, equal or unequal; corolla campanulate or funnelform, blue, lilac, or white (red in one species), deeply lobed, 5-dentate or almost entire; stamens and style included (exserted in one species), the pollen pantocolpate; style one, filiform, the 2 stigmas ellipsoid or oblong and complanate, ovary 2-locular, 4-ovulate, the disc small or none. *Fruits* capsular, globose to subglobose, 2-celled, with 4 or rarely 8 valves, 4-seeded; seeds glabrous, tuberculate, winged or pilose.

Robertson suggests that the genus contains about 100 species. The genus appears to be of American origin. *Convolvulus*, while closely allied, is distinguished by its filiform or subulate stigmas and forms the ecological equivalent in the Old World.

The ally of *Jacquemontia*, *Convolvulus nodiflorus* Desr. *in* Lam. (Encycl. Méth. Bot. 3: 557. 1789) (= *Jacquemontia nodiflora* (Desr.) G. Don (Hist. Dichl. Pl. 4: 283. 1838), is widely distributed in the West Indies, Central America and northern South America. It may be expected in Panama.

Literature:

Robertson, K. R. A revision of the genus *Jacquemontia* (Convolvulaceae) in North and Central America and the West Indies. Ph.D. dissertation, Washington University, St. Louis. 285 pp. 1971.

[4] Other synonyms were cited by Robertson (1971) under the genus *Jacquemontia* and under some of the species below. Only the names used here have been used for Panamanian material.

Sa'ad, F. The *Convolvulus* species of the Canary Isles, the Mediterranean Region and the Near and Middle East. Med. Bot. Mus. Herb. Rijksuniv. Utrecht 281(1967): 1–288. 1967.

a. Inflorescences dense head-like cymose clusters, the bracts large, foliaceous, densely reddish to yellowish pubescent.
  b. Bracts linear to lanceolate; corolla blue ..... 7. *J. tamnifolia*
  bb. Bracts broadly ovate to rounded; corolla white ..... 4. *J. hirtiflora*
aa. Inflorescences in lax or open cymes, the bracts small and inconspicuous, glabrous or pubescent, but pubescence not dense.
  c. Leaves sublinear to lanceolate, 7–15 mm wide.
    d. Sepals glabrescent, broadly ovate to subcordate, the outer 2 about ⅔ as broad as long ..... 3. *J. gracillima*
    dd. Sepals pubescent, often with glandular trichomes, lanceolate with a long acuminate apex, the outer 2 about ¼ as broad as long.
      e. Inflorescences lax; outer sepals lanceolate ..... 1. *J. agrestis*
      ee. Inflorescences condensed and subumbelliform; outer sepals subulate-lanceolate ..... 6. *J. sphaerostigma*
  cc. Leaves ovate to subcordate, 20–60 mm wide.
    f. Sepals obtuse, the interplicae pubescent; mostly with more than 2 flowers open per inflorescence at a time ..... 2. *J. ciliata*
    ff. Sepals lanceolate, the interplicae glabrous; usually 1–2 flowers open per inflorescence at a time.
      g. Corollas 2 cm long; glabrous or with appressed eglandular trichomes on sepals and pedicels ..... 5. *J. pentantha*
      gg. Corollas to 1.2 cm long; glandular trichomes on sepals and pedicels.
        h. Inflorescences lax; outer sepals lanceolate ..... 1. *J. agrestis*
        hh. Inflorescences condensed and subumbelliform; outer sepals subulate-lanceolate ..... 6. *J. sphaerostigma*

1. **Jacquemontia agrestis** (Mart. *ex* Choisy) Meisn. *in* Mart., Fl. Bras. 7: 306. 1869. *Convolvulus agrestis* Mart. *ex* Choisy *in* DC., Prodr. 9: 405. 1845. TYPE: Brazil, Bahia, St. Francisco, near Joazeiro, *Martius* (M, not seen; MO, photo).

Jacquemontia secundiflora (Fern.) O'Donell, Lilloa 26: 354. 1953. TYPE: Mexico, Guerrero, near Acapulco, *Palmer 32* (MO, isotype).
J. guatemalensis Standl. & Steyerm., Publ. Field Mus. Nat. Hist. Bot. Ser. 23: 84. 1944. TYPE: Guatemala, Chiquimula, *Steyermark 30066* (F, holotype, not seen).

Vines; stems erect when young, climbing or decumbent when mature, pubescent. *Leaves* broadly ovate to narrowly lanceolate, 1–5.5 cm long and 0.5–3.5 cm wide, basally cordate or subtruncate, apically acute to acuminate, rarely obtuse, with glandular and/or stellate indument. *Inflorescences* axillary, lax, 2–6-flowered monochasia, the peduncles pubescent. *Flowers* blue; sepals ovate, narrowly ovate or lanceolate, 3.5–6.5 mm long and 1–3 mm wide, attenuate, pubescent with glandular and/or stellate indument; corolla 0.6–1.2 cm long, interplicae glabrous; stamens unequal, the filaments basally glandular pubescent. *Fruits* capsular, subglobose, 4–5 mm in diameter, light brown, glabrous; seeds brown, 2–3 mm long, minutely areolate and strongly verrucate, with a small wing on the outer 2 margins.

This species flowers from September to March. It occurs from Arizona to Argentina and also in Cuba.

This species is often confused with *Jacquemontia sphaerostigma*. The best

way to distinguish them is by the inflorescence, lax in *J. agrestis* and subumbelliform in *J. sphaerostigma*. Apparently *J. agrestis* is represented in the different parts of its range by a number of variable populations. The species appears to be rare in Panama.

LOS SANTOS: Managre Beach 5 mi. SE of Chitré, *Tyson, Dwyer & Blum 2894* (MO).

2. **Jacquemontia ciliata** Sandwith, Kew Bull. 1930: 156. 1930. TYPE: Trinidad, Irois Forest, *Broadway 6718* (not seen).

Vines; stems herbaceous, pubescent with stellate trichomes. *Leaves* cordate, 2–11 cm long, basally cordate, apically acuminate to attenuate, pubescent. *Flowers* in axillary umbellate-cymose inflorescences, 8–11-flowered, pubescent; sepals elliptic, 5–7 mm long, ciliate; corollas white, sometimes with purple edges, or pale blue, 1.5–2.5 cm long, interplicae pubescent; stamens slightly unequal, the filaments basally pubescent; ovary conic-globose, glabrous. *Fruits* not seen.

This species flowers in November, February and March.

BOCAS DEL TORO: Changuinola Valley, *Dunlap 485* (US). Water Valley, Chiriqui Lagoon, *Wedel 1491, 1653, 1776* (all MO, US). CANAL ZONE: Around Las Cruces, *Pittier 2619* (F, US). COLÓN: Edge of Santa Rita Ridge ca. 20 mi. E of Colón, *Gentry 462* (MO). LOS SANTOS: 5 mi. S of Pocrí, *Croat 9736* (MO). PANAMÁ: Cerro Jefe, to 2900 ft, *Dwyer 8480* (MO).

3. **Jacquemontia gracillima** (Choisy) Hall. f., Bot. Jahrb. (Syst.) 16: 541. 1893.

Aniseia gracillima Choisy *in* DC., Prodr. 9: 430. 1845. SYNTYPE: Brazil, *Martius* (not seen).

Vines; stems herbaceous, pubescent. *Leaves* ovate-lanceolate to lanceolate, 1.5–3.5 cm long, basally acute, apically acute or lanceolate, glabrescent. *Flowers* in axillary racemose clusters, 2–3-flowered, pubescent; sepals ovate-cordate to suborbicular, 3–6 mm long and 3–6 mm wide, ciliate; corollas white, 5–10 mm long, interplicae glabrous; stamens unequal, the filaments basally pubescent; ovary conic-globose, glabrous. *Fruits* capsular, globose, enclosed within the sepals, 3–6 mm in diameter, glabrous, light brown; seeds light brown to red-brown, 2–4 mm long, spinulose and glabrous.

This species flowers in December. It occurs in Brazil and Panama.

COCLÉ: Aguadulce, *Pittier 4842* (F).

4. **Jacquemontia hirtiflora** (Mart. & Gal.) O'Donell, Ann. Inst. Biol. Méx. 12: 81. 1941.

Ipomoea hirtiflora Mart. & Gal., Bull. Acad. Bruxelles 12(2): 267. 1845. TYPE: Mexico, *Galeotti 1398* (G, not seen; photo in Robertson, 1971).

Jacquemontia perryana Duchass. & Walp., Linnaea 23: 751. 1850. TYPE: Panama, *Duchassaing* (not seen).

Ipomoea lactescens Seem., Bot. Voy. Herald 171. 1854. SYNTYPE: Panama, *Seemann s.n.*; *Cuming 1158* (neither seen).

Jacquemontia platycephala Donn. Sm., Bot. Gaz. (Crawfordsville) 57: 423. 1914. TYPE: Guatemala, *Tuerckheim 4133* (not seen).

Maripa volubilis Pittier, Bol. Soc. Venez. Cienc. Nat. 6: 199. 1940. TYPE: Venezuela, Monagas, *Pittier 14381* (US, lectotype).

Vines; stems herbaceous, hirsute to glabrescent. *Leaves* rounded-ovate to deltoid-ovate, 6–13 cm long, basally cordate, apically acuminate, glabrous to short-pilose above, appressed pilose beneath, glabrate. *Inflorescence* of capitulate clusters; peduncles longer than the leaves; bracts to 2 cm long, orbicular, rounded to obtuse apically, densely hirsute. *Flowers* with the sepals elliptic, acuminate, 12 mm long, yellowish to reddish hirsute; corolla white, 3–4 cm long, funnelform, the interplicae villous; stamens unequal, the filaments 4–6 mm long; style 10 mm long. *Fruits* capsular, broadly conical, 10 mm in diameter, black, glabrous; seeds 4, tan to orange, 4–5 mm long, glabrous.

This species flowers from October to April. It is reported from Southern Mexico, British Honduras, Guatemala, Costa Rica, Panama, Colombia and Venezuela.

CANAL ZONE: Farfan Beach, *Burch et al. 1413* (MO). Near Paraíso, *Croat 7150* (MO). 1 mi. NW of Summit Gardens, *Croat 8887* (MO). Madden Forest Road, *Croat 8930* (MO). 1 mi. N of Summit Gardens, *Croat 9082* (MO). Gamboa, *Dwyer 6568* (MO). Cocoli, *Dwyer 7222* (MO). Albrook, U. S. Army Test Center, *Dwyer 7316* (MO). Albrook, *Dwyer & Robyns 67* (MO). Near Arraijan checkpoint, *Dwyer et al. 4352* (MO). Without locality, *Eppelsheimer 1910* (F). E of Curundu, *Harvey 5202* (F). W of Curundu, *Harvey 5236* (F). Between Gamboa and Summit Gardens, *Kennedy 2261* (MO). Panama-Cruces Trail, *Killip 3251* (US); *Nowicke et al. 3602* (MO). Juan Mina, *Piper 5687* (US). Río Grande, near Culebra, *Pittier 2132* (US). Empire to Mandinga, *Pittier 5439, 5474* (both US). Balboa, *Standley 25536, 26094* (both US). Summit, *Standley 26918* (US). Frijoles, *Standley 27616* (US). Corozal, *Standley 27355* (US). Gamboa, *Standley 28430* (US). Río Pedro Miguel, near E. Paraíso, *Standley 30036* (US). Obispo, *Standley 31659* (US). 1 mi. N of Summit Garden, *Tyson & Blum 1979* (MO). 1 mi. N of Summit on road to FAA tower, *Tyson et al. 2747* (MO). Frijoles, *Woodworth & Vestal 742* (MO). DARIÉN: Around Garachiné, *Pittier 5518* (US). Tucutí, Chepigana, *Terry & Terry 1371* (F, MO). HERRERA: Between Las Minas and Pesé, *Burch et al. 1326* (MO). PANAMÁ: Sabanas near Chepo, *Hunter & Allen 73* (MO). Sabanas, *Hunter & Allen 17071* (MO). Between Savanas and Río Yguana, *Macbride 2649* (F, US). Matías Hernández, *Pittier 6915* (US). Between Matías Hernández and Juan Díaz, *Standley 32018* (US). VERAGUAS: W of Sona, *Allen 1028* (MO). Cañazas, *Tyson 3610* (MO).

5. **Jacquemontia pentantha** (Jacq.) G. Don, Hist. Dichl. Pl. 4: 283. 1838.[5]

Convolvulus pentanthus Jacq., Coll. Bot. 4: 210. 1780. TYPE: Herb. Jacquin (W).
C. violaceus Vahl, Symb. Bot. 3: 29. 1794, non Spreng. (1824). TYPE: not seen.
Jacquemontia azurea (Desr.) Choisy, Mém. Soc. Phys. Genève 6: 467. 1833. TYPE: not seen.
J. violacea (Vahl) Choisy, Mém. Soc. Phys. Genève 8: 139. 1839.
J. azurea var. *alba* Seem., Bot. Voy. Herald 172. 1854. TYPE: Panama, *Seemann* (BM, not seen; MO, photo).
J. violacea var. *guatemalensis* Meisn. *in* Mart., Fl. Bras. 7: 296. 1869. TYPE: Guatemala, *Friedricksthal* (not seen).

Vines; stems herbaceous, pubescent to glabrate. *Leaves* ovate to broadly ovate, 3–6 cm long, basally cordate, apically acuminate, glabrate. *Inflorescences* dense cymes on peduncles mostly longer than the leaves, mostly 1–2-flowered at any time. *Flowers* with the sepals ovate to lanceolate, acute to acuminate 4–5 mm long and 2–4 mm wide, pubescent; corolla mostly blue, sometimes white, 2 cm long, interplicae glabrous; stamens slightly unequal, the filaments glandular pubescent; ovary oblong, glabrous. *Fruits* capsular, globose, 4 mm in diameter, glabrous; seeds brown, 2.5 mm long, glabrous.

[5] Other synonyms were cited by Robertson (1971). Only the names cited here have been used for Panamanian material.

This species flowers from December to March. It occurs in Florida, Mexico, Guatemala, British Honduras, Costa Rica, Panama, the West Indies and South America.

CANAL ZONE: Farfan Beach, *Burch et al. 1415* (MO). Albrook, *Dwyer 7312* (MO). E of Curundu, *Harvey 5201* (F). W of Curundu, *Harvey 5237* (F). Las Cruces Trail, *Hunter & Allen 765, 781* (both MO). Farfan Beach, *Lewis et al. 45* (MO). Near Corozal, *Piper 5306, 5314* (both US). Chiva-Chiva Trail, *Piper 5765* (US). Around Culebra, *Pittier 2151* (US). El Paraiso, *Pittier 2520* (US). N of Gamboa, *Robyns 65-45* (MO, US). Summit, *Standley 26961* (US). Las Cruces Trail, *Standley 29020, 29086* (both US). Above E. Paraiso, *Standley 29902* (US). Summit, *Standley 30148* (US). Farfan Beach, *Tyson & Blum 2612* (MO). COCLÉ: Road to El Cope, *Burch et al. 1368* (MO). 3 mi. NE of Antón, *D'Arcy & Croat 4103* (MO). DARIÉN: Near Punta Garachiné, *Duke 10479* (MO). Patiño, *Duke 10538* (MO). HERRERA: Chitré, *Allen 1102* (MO). Near Ocú, *Allen 4078* (MO). Río Sta. Maria, *Burch et al. 1185* (MO). Near River at Ocú, *Croat 9647* (MO). 10 mi. S of Ocú, *Tyson et al. 2875* (MO). LOS SANTOS: 5–9 mi. from Chitré, *Burch et al. 1218* (MO). Roadside from Las Tablas, *Burch et al. 1273* (MO). PANAMÁ: Near Juan Díaz, *Killip 3340* (US). Near Aguarumbia, *Killip 3355* (US). Between Savanas and Río Yguana, *Macbride 2653* (F, US). Panama La Vieja, *Bro. Paul 789* (US). Matías Hernández, *Pittier 6947* (US). Near Matías Hernández, *Standley 28970* (US). Tumba Muerto Road, *Standley 29800* (US). Between Las Sabanas and Matías Hernández, *Standley 31807* (US). Between Matías Hernández and Juan Díaz, *Standley 32001* (US). Penonomé, *Williams 190* (US). VERAGUAS: 8 mi. W of Santiago, *Tyson 6079* (MO).

6. **Jacquemontia sphaerostigma** (Cav.) Rusby, Bull. Torrey Bot. Club 26: 151. 1899.—FIG. 4.

Convolvulus sphaerostigma Cav., Icon. 5: 54, *t. 481*. 1799. TYPE: Mexico, *Cavanilles* (not seen).

Vines; stems herbaceous, sprawling or twining, pubescent. *Leaves* ovate-lanceolate, 1–3 cm long and 0.5–1 cm wide, basally rounded to obtuse, apically acute to attenuate, stellate-pubescent. *Inflorescences* axillary umbellate cymes, 2–6 flowers per inflorescence, pubescent. *Flowers* with the sepals attenuate-elliptic to lanceolate, 4–7 mm long and 1–2 mm wide, mostly attenuate, pubescent; corollas blue, 0.4–1 cm long, interplicae glabrous; stamens unequal, the filaments basally glabrous. *Fruits* capsular, globose, 3–4 mm in diameter, light brown, glabrous; seeds red-brown, 2 mm long, glabrous.

This species flowers from October to January. It occurs in Mexico, British Honduras, Guatemala, Honduras, Costa Rica, Panama, Venezuela, Peru, Bolivia and Brazil.

CANAL ZONE: Balboa, *Standley 26098* (US). Between Fort Clayton and Corozal, *Standley 29162* (US). Balboa, *Standley 29307* (US). COCLÉ: S of El Valle de Antón, *Allen 2808* (US). PANAMÁ: Tumba Muerto, *Bro. Heriberto 197* (US). NE of Panama City, *Bro. Paul 192* (US). Near Panamá, *Standley 27763, 29778* (both US).

7. **Jacquemontia tamnifolia** (L.) Griseb., Fl. Brit. W. Ind. 474. 1861.

Ipomoea tamnifolia L., Sp. Pl. 162. 1753. LECTOTYPE: *Dillenius*, Hort. Eltham. *t. 318, f. 410.* ***Thyella tamnifolia*** (L.) Raf., Fl. Tellur. 4: 84. 1836.

Vines; stems herbaceous, hirsute throughout. *Leaves* ovate to broadly ovate, 3–10 cm long and 1.5–6 cm wide, basally cordate, apically acute or abruptly acuminate, glabrescent. *Flowers* in dense head-like cymose inflorescences, many-

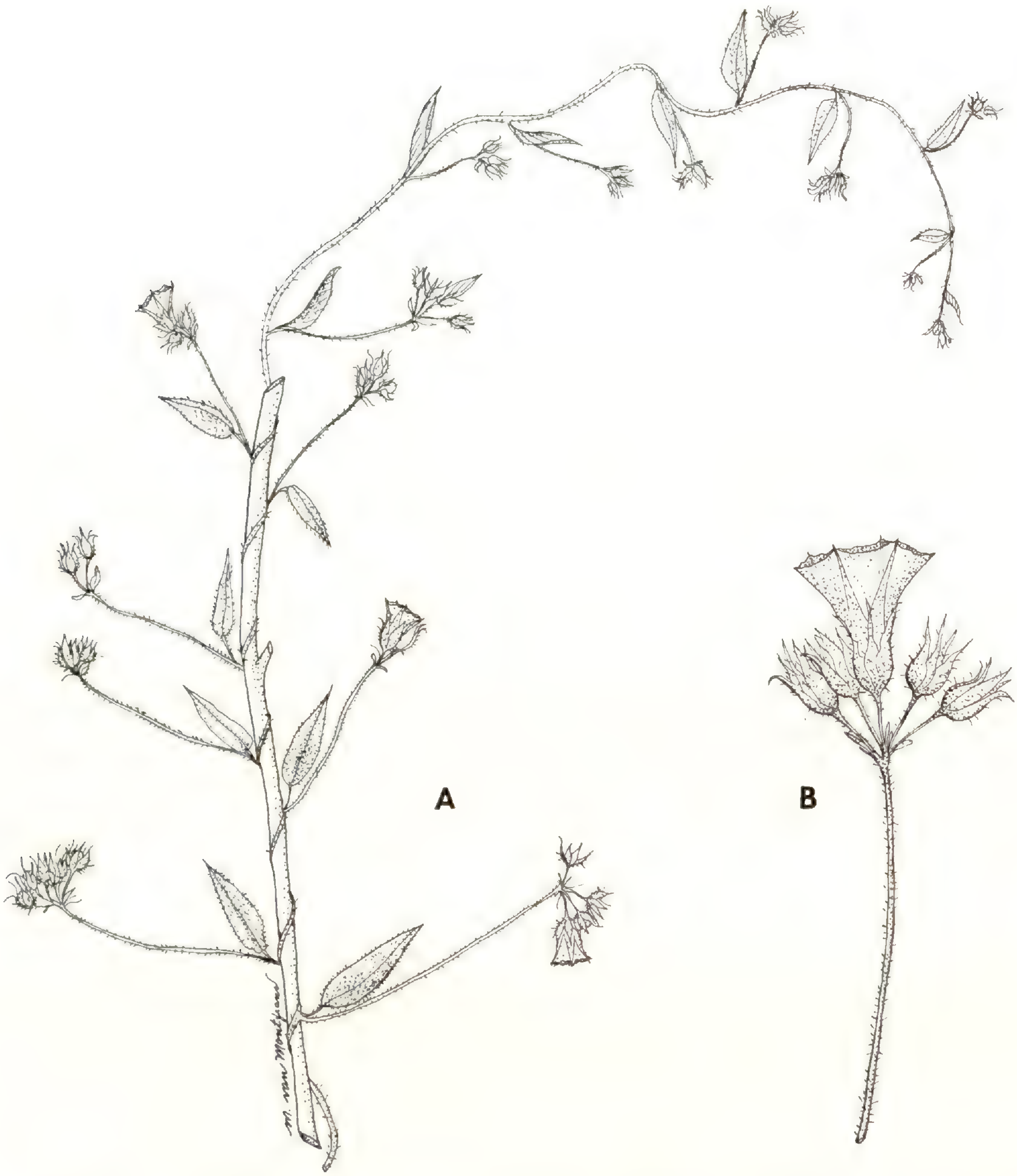


FIGURE 4. *Jacquemontia sphaerostigma* (Cav.) Rusby.—A. Habit (× ½).—B. Inflorescence (× 1½). [After *Piper 5555* (US).]

flowered but few open at one time, densely hirsute; sepals lanceolate, 10–15 mm long and 1–3 mm wide, acuminate, hirsute with yellowish brown trichomes; corollas mostly blue, some white, 1 cm long, interplicae glabrous; stamens subequal, the filaments basally glabrous; ovary subglobose, glabrous. *Fruits* capsular, enclosed in sepals and subfoliose bracts, globose, 4–5 mm in diameter, light brown, glabrous; seeds orange-brown, 2.5 mm long, glabrous.

This species flowers from October to February. It occurs in the southeastern United States, Mexico, Guatemala, British Honduras, Honduras, Panama and in the Greater Antilles.

CANAL ZONE: E of Fort Clayton, *Harvey 5104* (F). E of Curundu, *Harvey 5210* (F). Between Farfan Beach and Palo Seco, *Hunter & Allen 439* (MO). Balboa, *Standley 26089, 26099* (both US). Corozal, *Standley 27379* (US). Balboa, *Standley 29309* (US). COCLÉ: Near Ola, *Pittier 5095* (US). PANAMÁ: Near Bejuco, *Allen 977* (MO). NE of Hacienda La Joya, *Dodge et al. 16894* (MO). First bend of Río Pasiga, *Gentry 2378* (MO). San José Island, *Johnston 175* (US). Río Tapia, *Standley 28163* (US). Tumba Muerto Road, *Standley 29774* (US). VERAGUAS: 1–2 mi. above Santa Fé, *Gentry 3068* (MO).

5. EVOLVULUS

Evolvulus L., Sp. Pl., ed. 2. 391. 1762; Gen. Pl., ed. 6. 152. 1764. TYPE: *E. nummularius* L.

Herbs or small suffrutescent shrubs, annual or perennial, not twining but sometimes creeping. *Leaves* usually small, ovate to almost linear, entire. *Flowers* in axillary, pedunculate, 1- to several-flowered dichasia or solitary, pedunculate or sessile in the leaf axils; sepals 5, free, equal or subequal; corolla small to medium, conspicuous blue or inconspicuous faded bluish-white, rotate, funnelform or salverform, the limb plicate, mostly subentire, the interplicae pilose outside; stamens 5, the filaments filiform, inserted within the corolla tube, the anthers ovate to oblong or linear, pollen pantocolpate; ovary 2-loculate, each locule biovulate, sometimes 1-locular and 4-ovulate; styles 2, free or basally united, each style deeply bifid for at least half its length, stigmas long, terete, filiform to subclavate. *Fruits* capsular, globose to ovoid, 4-valvate, (1–)4-seeded; seeds small, smooth or minutely verrucose, the cotyledons almost flat, the radicle incurved.

The 100 species of this genus have not been studied in detail since van Oostroom's monograph (1934). Some of the many species and varieties he recognized seem tenuous on the basis of herbarium material. Field examination in Florida and the West Indies indicates that some of these forms may be autogamous.

Literature:

Ooststroom, S. J. van. A monograph of the genus *Evolvulus*. Med. Bot. Mus. Herb. Rijksuniv. Utrecht 14: 1–267. 1934.

a. Leaves broadly oval, orbicular to oblong, the apex obtuse; plants prostrate, rooting at the nodes ..... 3. *E. nummularius*
aa. Leaves oblong-ovate, elliptical to sublinear, the apex acute to acuminate; plants prostrate, reclinate to erect, rarely rooting at nodes.
b. Inflorescences not pedunculate, the flowers solitary to fasciculate from leaf axils.
c. Leaves oblong-ovate; stems pubescent with long, reddish, spreading trichomes ..... 4. *E. ovatus*
cc. Leaves linear to oblong; stems covered with appressed white or reddish trichomes or glabrescent ..... 5. *E. sericeus*
bb. Inflorescences pedunculate, axillary or sometimes terminal.
d. Pubescence of stems spreading.
e. Corollas 10–15 mm broad ..... 6. *E. tenuis*
ee. Corollas 3–7 mm broad ..... 1. *E. alsinoides*
dd. Pubescence of stems appressed or apparently wanting ..... 2. *E. filipes*

1. **Evolvulus alsinoides** (L.) L., Sp. Pl., ed. 2. 392. 1762.

Convolvulus alsinoides L., Sp. Pl. 157. 1753. LECTOTYPE: Ceylon, Herb. Hermann 3: 55 (BM, not seen).
C. linifolius L., Syst. Nat., ed. 10. 923; Amoen, Acad. 4: 306. 1759. LECTOTYPE: Senegal, (LINN, 393.5, not seen; microfiche).
Evolvulus linifolius (L.) L., Sp. Pl., ed. 2. 392. 1762.

Herbs; stems herbaceous or suffrutescent, reclining or ascending, pubescent with spreading trichomes. *Leaves* oblong, elliptic-oblong or lanceolate, 1–2.5 cm long, mostly less than 1 cm wide, subsessile, acute to obtuse basally and apically, pubescent. *Flowers* on peduncles mostly equaling the leaves; sepals lanceolate, acute or acuminate, 2–3 mm long, pubescent; corollas mostly pale blue, sometimes white, 3–7 mm broad; ovary glabrous. *Fruits* capsular, globose, glabrous; seeds black, smooth.

This species flowers from March to August and in December. It ranges from the southern United States through Central America and into South America. It is widely dispersed in the Old World tropics.

Ooststroom (1934) recognized a number of varieties in this species complex. Differences between the named populations are subtle. In Panama I have seen material from only var. *debilis* (H.B.K.) Ooststr.

CANAL ZONE: Balboa, *Standley 26436* (US). CHIRIQUÍ: Llano de Volcán, *Allen 4848* (US). 1 mi. N of El Hato del Volcán, *Croat 10692* (MO). Boquete, *Davidson 662* (MO, US); *Lewis et al. 368* (MO). Near El Boquete, *Maxon 5143* (US). El Boquete, *Pittier 3155* (US). Llano del Volcán, *Seibert 344* (MO). Llanos Francia, Boquete, *Stern et al. 1221* (MO). El Volcán, *Tyson 5828* (MO). COCLÉ: Aguadulce, *Pittier 4879* (US). HERRERA: Ocú, *Ebinger 1093* (MO).

2. **Evolvulus filipes** Mart., Flora 24, Beibl. 2: 100. 1844. TYPE: Brazil, Bahia, Rio S. Francisco near Joazeiro, *Martius* (not seen).

Annual *herbs*; stems erect to ascending, delicate, usually sparsely appressed pubescent. *Leaves* linear to narrowly lanceolate, 1–2.5 cm long and mostly 2–5 mm wide, sessile to subsessile, acute apically and basally, sparsely pilose above, slightly more pubescent beneath. *Flowers* on peduncles mostly equaling or longer than leaves; sepals lanceolate, 2–2.5 mm long, glabrous to pubescent outside, ciliate; corollas pale blue or white, 3–5 mm broad; ovary glabrous. *Fruits* capsular, globose or ovoid, reflexed; seed dark brown to black, smooth.

Evolvulus filipes flowers from October to January. It occurs in Mexico, Central America, South America and Jamaica.

This species and *E. alsinoides* are similar. The flowers of *E. filipes* tend to be smaller, and the entire plant is more delicate in appearance than *E. alsinoides*.

CANAL ZONE: Balboa, *Standley 25293* (US). Las Cruces Trail, *Standley 29188* (US). COCLÉ: Aguadulce, *Pittier 4841* (US). HERRERA: Near Chitré, *Allen 1087* (MO). PANAMÁ: Between Capira and Potrero, *Dodge & Allen 8612* (MO). Punta Paitilla, *Bro. Heriberto 230* (US). Sabanas near Chepo, *Hunter & Allen 17* (F, MO, US). Sabanas, *Hunter & Allen 58* (MO). San José Island, *Johnston 318, 946* (both MO, US). Aihajuela, *Killip 3223* (US). Sabanas, *Bro. Paul 223* (US); *Pittier 2536* (US). Sabana de Dormisolo, *Pittier 4666* (US). Matías Hernández, *Pittier 6922* (US). Bella Vista, *Standley 25365* (US). Near Punta Paitilla,

Standley 26297 (US). E of Río Tocumen, *Standley 26634* (US). Near Juan Franco Race Track, *Standley 27765* (US). Río Tocumen, *Standley 29406* (US). Nuevo San Francisco, *Standley 30700* (US).

3. **Evolvulus nummularius** (L.) L., Sp. Pl., ed. 2. 391. 1762.—Fig. 5.

Convolvulus nummularius L., Sp. Pl. 157. 1753. LECTOTYPE: West Indies, Jamaica, *Sloane* (BM, not seen).
Volvulopsis nummularium (L.) Roberty, Candollea 14: 28. 1952.

Perennial *herbs*; stems prostrate, herbaceous, rooting at nodes, pilose with short trichomes to glabrate. *Leaves* broadly ovate to orbicular, 4–15 mm long, short-petiolate, rounded to emarginate apically, rounded to subcordate basally, glabrous or somewhat pubescent beneath. *Flowers* solitary or paired in leaf axils, pedicels 2–6 mm long; sepals elliptic-ovate to ovate-oblong, 2.5–4 mm long, pubescent, glabrescent, ciliate; corollas white, 5–7 mm broad; ovary glabrous. *Fruits* capsular, globose, 3–4 mm in diameter, reflexed; seeds brown to black, subglobose, slightly muricate.

Flowering probably all year, the specimens seen were taken from October to July. The species occurs in Mexico, Central America, West Indies, South America and the Old World tropics.

CANAL ZONE: Fort San Lorenzo, *Burch et al. 1022* (MO). Tivoli Hotel, *D'Arcy 3954A* (MO). Fort Kobbe, *Duke 3908* (MO). Miraflores Bridge, *Dwyer 1057* (MO). Ancon Hill, *Killip 12190* (US); *Piper 5493* (US). Miraflores Lake, *White 271* (MO). CHIRIQUÍ: David airport, *Lewis et al. 767* (MO). COCLÉ: Río Hato, *Burch et al. 1151* (MO). DARIÉN: El Real, *Burch et al. 1055* (MO). LOS SANTOS: 5–9 mi. from Chitré, *Burch et al. 1215* (MO). PANAMÁ: Las Sabanas, *Bro. Heriberto 205* (US). Near Chepo, *Hunter & Allen 12* (MO). Panama City, *Killip 3047* (US). La Chorrera, *Lewis et al. 5187* (MO). Panama Golf Course, *Piper 6013* (US). Chepo, *Pittier 4459* (US). Laguna de Portala near Chepo, *Pittier 4609* (US). Las Sabanas, *Standley 25830* (US). E of Río Tocumen, *Standley 26669* (US). Río Tapia, *Standley 28144* (US). Near Matías Hernández, *Standley 28899* (US). Nuevo San Francisco, *Standley 30724* (US).

4. **Evolvulus ovatus** Fern., Proc. Amer. Acad. Arts 33: 89. 1898. TYPE: Mexico, near Acapulco, *Palmer 313* (not seen).

Annuals *herbs*; stems erect, pubescent with long spreading trichomes. *Leaves* oblong-ovate, 1–5 cm long, subsessile to sessile, rounded to cordate basally, obtuse to acute apically, pubescent on both surfaces with long spreading trichomes. *Flowers* 1–2 in the leaf axils; sepals lanceolate, 4–5 mm long, pilose; corollas blue, 5 mm broad; ovary glabrous. *Fruits* capsular, depressed-globose to ovoid, 3–4 mm in diameter, reflexed; seeds dark brown, smooth.

Evolvulus ovatus flowers in December. It occurs in Mexico, Guatemala, Panama, Colombia, Venezuela and Brazil.

The single collection from Panama may best be referred to f. *oblongus* Ooststr. (1934), but it does not match in all characteristics.

COCLÉ: Aguadulce, *Pittier 4886* (US).

5. **Evolvulus sericeus** Swartz, Prod. Veg. Ind. Occ. 55. 1788. TYPE: not seen.

Perennial *herbs*; stems decumbent to erect, herbaceous, usually grey-sericeus. *Leaves* linear, linear-lanceolate to elliptic, 1–2.5 cm long and 1–8 mm wide,

A
B
C
D
H Cuddy

sessile to subsessile, pubescent at least on the lower surface, sometimes glabrous above. *Flowers* usually solitary in the leaf axils, occasionally 2 or more; sepals oblong-lanceolate to lanceolate, 3–5 mm long, pubescent; corollas white or pale blue, 7–12 mm broad; ovary glabrous. *Fruits* capsular, globose to ovoid, 4–5 mm in diameter, reflexed, seeds brown, smooth.

Evolvulus sericeus flowers from December to July. It occurs from Mexico to Panama, in the West Indies and in South America.

This species is most commonly confused with *E. alsinoides*. They may be distinguished by the long-pedunculate inflorescences of *E. alsinoides* and the non-pedunculate, but pedicellate flowers of *E. sericeus*.

COCLÉ: Near Santa Clara Beach, *Croat 9604* (MO). E of Natá, *Duke 12399* (MO). La Pintada, *Hunter & Allen 525* (F). Between Porto Posada and Penonomé, *Williams 181* (US). PANAMÁ: Near Playa Río Mar, *Duke 11759* (MO); *Ebinger 506* (MO). Near Juan Franco Race Track, *Standley 27815* (US).

6. **Evolvulus tenuis** Mart. *ex* Choisy, Mém. Soc. Phys. Genève 8: 78. 1839. TYPE: Brazil, Rio Dove, *Martius* (not seen).

Herbs, sometimes suffruticose; stems erect to ascending, densely pubescent with long trichomes. *Leaves* ovate to oblong-ovate, 1.5–3.5 cm long and 1–2 cm wide, acute to acuminate apically, acute basally, pubescent to glabrate. *Flowers* on peduncles mostly equaling or longer than leaves; sepals lanceolate, acuminate, 2.5–3 mm long, pubescent; corollas blue to white, 10–15 mm broad. *Fruits* globose to ovoid, glabrous; seeds not seen.

This species flowers in March. It is known from Yucatan to South America. The specimens most closely match subsp. *longifolius* (Choisy) Ooststr.

CANAL ZONE: Summit Garden, cultivated, *Croat 10288* (MO). PANAMÁ: Panama City, *Maurice 765* (US). Sabanas, *Bro. Paul 553* (US).

4. "MERREMIOIDS"

This grouping of genera appears natural, but I do not wish to apply a formal name to them without further study. The genera under the term "merremioids" exhibit numerous shared characteristics which separate them from other tribal groups. Detailed study of the literature is necessary before a correct tribal name can be determined.

6. MERREMIA

Merremia Dennstedt, Schluss Hort. Malab. 34. 1818. TYPE: *M. hederacea* (Burm. f.) Hall. f. = *M. convolvulacea* Dennst.

Skinnera Choisy, Mém. Soc. Phys. Genève 6: 487. 1833, non Forst. (1776). TYPE: *S. caespitosa* Choisy = *Merremia hirta* (L.) Merrill.
Spiranthera Bojer, Hort. Maurit. 226. 1837, nomen nudum, non St. Hil. (1823).

←

FIGURE 5. *Evolvulus nummularius* (L.) L.—A. Habit (×2).—B. Flower (×5).—C. Gynoecium (×7½).—D. Fruit (×5).

Vines or lianas; usually herbaceous, some lignescent, small or large. *Leaves* entire, lobed, or palmately compound with 3–7 leaflets, glabrous or pubescent. *Flowers* solitary and axillary, in few-flowered dichasia or sub-umbellate, the bracts linear or lanceolate; sepals subequal, oblong to elliptical; corolla campanulate, large or small, white, yellow or purple; the filaments equal or subequal, mostly glabrous at the base, the anthers spirally twisted with complete dehiscence, the pollen 3-colpate or rarely pantocolpate; ovary usually glabrous, 2–3 carpellate, 4–6 ovulate, the style filiform, the stigma globose or biglobose, included. *Fruits* capsular, 2–4-celled, longitudinally dehiscent by 4–6 valves or irregularly, the pericarp thin and fragile; the seeds 4–6, glabrous or pubescent.

A tropical and subtropical genus of 60–80 species. Except for a study of the Brazilian members of the genus by Falcão (1954), there has been little study of the American species since O'Donell's (1941) revision.

Literature:

O'Donell, C. A. Revision de las especies Americanas de *Merremia.* Lilloa 6: 467–554. 1941.

Falcão, J. Contribuição ao estudo das espécies Brasileiras do gênero *Merremia* Dennst. Rodriguesia 16–17: 105–114. 1954.

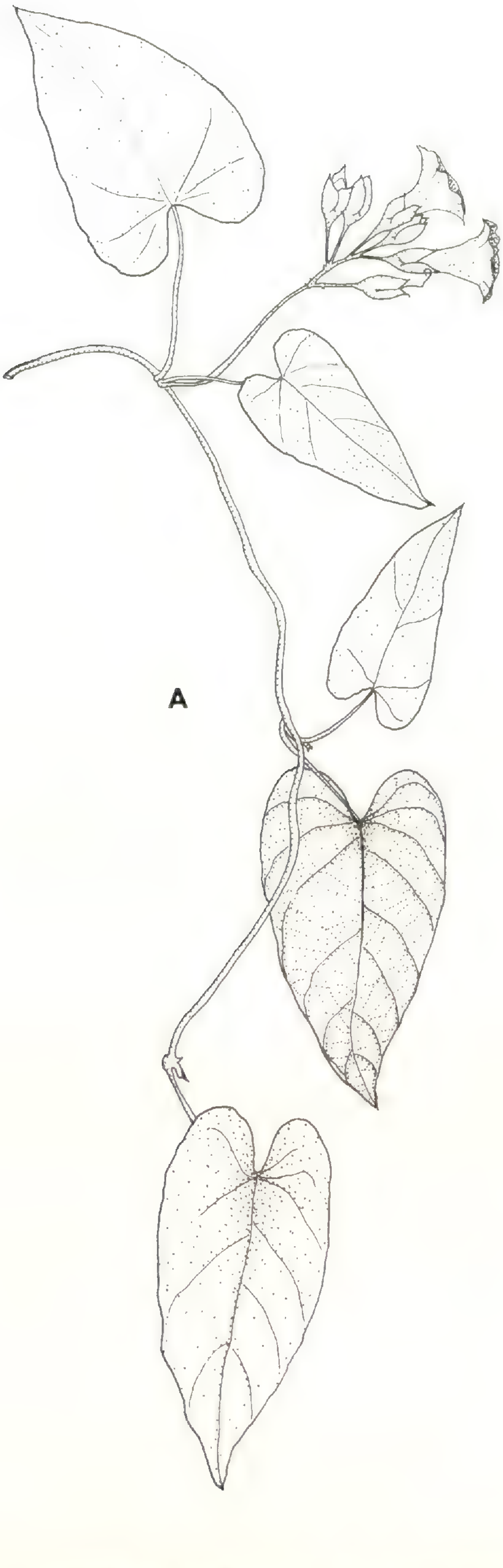
a. Leaves entire; inflorescences umbellate ---------- 5. *M. umbellata*
aa. Leaves deeply lobed to subpalmately compound; inflorescences dichasial.
b. Leaves deeply lobed but not compound, the lobes connected by some tissue at the base.
c. Lobes of leaves entire; flowers yellow, broadly funnelform to subcampanulate ---------- 4. *M. tuberosa*
cc. Lobes of leaves crenate; flowers white with purplish to reddish centers, broadly campanulate ---------- 2. *M. dissecta*
bb. Leaves palmately compound, the segments distinct.
d. Sepals and stems densely pubescent with erect yellowish, eglandular trichomes ---------- 1. *M. aegyptia*
dd. Sepals and stems glabrous or with glandular trichomes on the sepals ---------- 3. *M. quinquefolia*

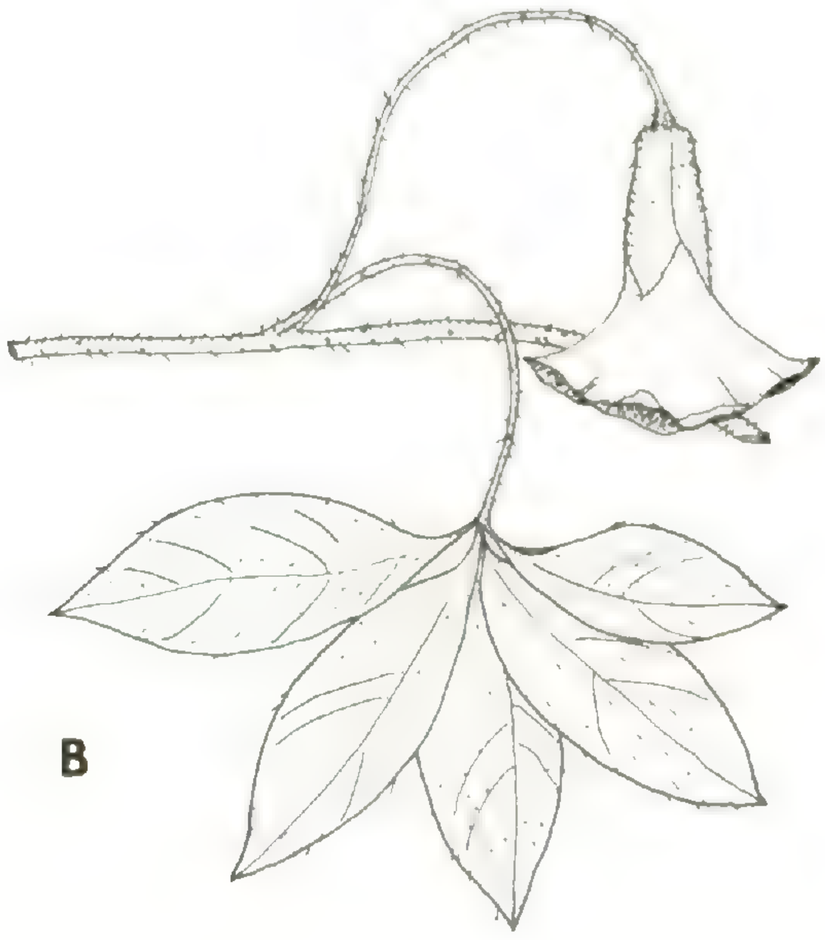
1. **Merremia aegyptia** (L.) Urb., Symb. Antill. 4: 505. 1910.—FIG. 6B, D.

Ipomoea aegyptia L., Sp. Pl. 162. 1753. TYPE: not seen.
Convolvulus pentaphyllus L., Sp. Pl., ed. 2. 223. 1762. TYPE: West Indies (not seen).
Ipomoea pentaphylla (L.) Jacq., Coll. Bot. 2: 297. 1788.
Merremia pentaphylla (L.) Hall. f., Bot. Jahrb. (Syst.) 16: 552. 1893.
Operculina aegyptia (L.) House, Bull. Torrey Bot. Club 33: 502. 1906.

Vines; stems herbaceous, mostly hirsute with long erect to suberect yellowish trichomes. *Leaves* palmately compound, the 5 leaflets elliptic, entire to dentate, acuminate to acute apically and basally, sparsely pubescent to glabrate. *Flowers* cymose on long peduncles; sepals oblong, 2 cm long, acute, hirsute with erect yellowish trichomes; corollas white with a purple center, 2–3 cm long. *Fruits* capsular, subglobose, 1–2 cm in diameter, subtended and partially surrounded by the calyx; seeds black, glabrous.

The species flowers from October to February. It ranges from Mexico to Panama, the West Indies, South America and the Old World tropics.





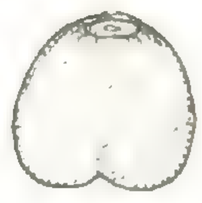


FIGURE 6. *Merremia*.—A. *M. umbellata* (L.) Hall. f., habit (× ½).—B. *M. aegyptia* (L.) Urb., stem section (× ½).—C. *M. umbellata*, seed (× 2½).—D. *M. aegyptia*, seed (× 2½).—E. *M. dissecta* (Jacq.) Hall. f., stem section (× ½). [A after *Croat 8050* (MO). B after *Burch et al. 1292* (MO). C after *Dunlap 355* (F). D after *Macbride 2786* (F). E after *Adams & Adams s.n.* (FAU).]

CANAL ZONE: Near E. Paraíso, *Standley 30032* (US). COCLÉ: Banks of Río Grande, *Burch et al. 1177* (MO). 10 mi. E of Natá, *Tyson 5219* (MO). DARIÉN: Near Vera Cruz, *Duke 6167A* (MO). HERRERA: Between La Avena and Pesé, *Burch et al. 1292* (MO). PANAMÁ: Taboga Island, *Macbride 2786* (F, US). Between Las Sabanas and Matías Hernández, *Standley 31918* (US).

2. **Merremia dissecta** (Jacq.) Hall. f., Bot. Jahrb. (Syst.) 16: 552. 1893.—FIG. 6E.

Convolvulus dissectus Jacq., Obs. Bot. 2: 4, *t.* 28. 1767. TYPE: *Jacquin* (not seen).
Ipomoea sinuata Ortega, Hort. Matr. Dec. 7: 84. 1798. TYPE: (not seen).
Operculina dissecta (Jacq.) House, Bull. Torrey Bot. Club 33: 500. 1906.
Ipomoea dissecta (Jacq.) Pursh, Fl. Amer. Sept. 145. 1814.

Vines; stems herbaceous, sparsely hirsute to glabrous. *Leaves* palmately divided almost to the base, the 7–9 lobes sinuate to sinuate-dentate, usually glabrous. *Flowers* usually solitary, occasionally in cymes; sepals oblong, 18–25 mm long, mucronate, glabrous; corollas white with a purple center, 3–4.5 cm long. *Fruits* capsular, depressed-globose, 1–2 cm in diameter, subtended and partially surrounded by the calyx; seeds black, glabrous.

This species flowers from July to August. It occurs in Florida, the West Indies, Mexico, Central America and South America.

BOCAS DEL TORO: Isla Colón, *Wedel 508* (MO). CANAL ZONE: Without locality, *Applesheimer, 1910* (F). CHIRIQUÍ: 1 mi. W of Puerto Armuelles, *Croat 22032* (MO).

3. **Merremia quinquefolia** (L.) Hall. f., Bot. Jahrb. (Syst.) 16: 552. 1893.

Ipomoea quinquefolia L., Sp. Pl. 162. 1753. TYPE: Based on *Convolvulus quinquifolius glaber Americanus* Pluk., Alm. 2116, *t. 167, f. 1* [6], 1696.

Lianas; stems herbaceous toward the tips, woody and perennial basally, usually glabrous. *Leaves* 5-foliolate, the leaflets subsessile, elliptic, lanceolate to oblanceolate, acute or acuminate apically and basally, glabrous. *Flowers* solitary or a simple cyme, rarely a compound cyme; sepals oblong, the outer 3–5 mm long, the inner 4–7 mm long, obtuse, glabrous; corollas completely white, 1.5–2.5 cm long. *Fruits* capsular, subglobose, partially subtended by sepals, 7–8 mm broad; seeds pubescent.

This species flowers in December, January and April. It occurs in southern Florida, the West Indies, Mexico, Central America and South America.

CANAL ZONE: Ancón, *Greenman & Greenman 5012* (MO). Between Miraflores and Pedro Miguel, *Pittier 2500* (US). Gamboa, *Standley 28451* (US). Darién Station, *Standley 31561* (US). CHIRIQUÍ: 1 mi. W of airport at Puerto Armuelles, *Croat 21893* (MO). HERRERA: Banks of Río Santa Maria, *Burch et al. 1191* (MO). LOS SANTOS: 5–9 mi. from Chitré, *Burch et al. 1217* (MO). PANAMÁ: Vera Cruz, *Lewis et al. 3001* (MO). Cerro Campana, *Lewis et al. 3107* (MO). Taboguilla Island, *Miller 2010* (US). Sabanas, *Bro. Paul 288* (US). Juan Díaz, *Standley 30484* (US).

4. **Merremia tuberosa** (L.) Rendle *in* Thist.-Dyer, Fl. Trop. Africa 4: 104. 1905.

Ipomoea tuberosa L., Sp. Pl. 160. 1753. LECTOTYPE: Herb. Linn. (LINN 219.4, not seen; microfiche).

Operculina tuberosa (L.) Meisn. *in* Mart., Fl. Bras. 7: 212. 1869.

Lianas; stems herbaceous toward the tips, basally woody, glabrous. *Leaves* usually 7-lobed, at times almost to the base, the lobes lanceolate to elliptic, acuminate, entire, glabrous. *Flowers* in compound cymes with peduncles 10–20 cm long, occasionally solitary; sepals unequal, the outer oblong, 25–30 mm long, obtuse, mucronulate, the inner smaller, 12–20 mm long, acute; corollas yellow, 5–6 cm long. *Fruits* capsular but irregularly dehiscent, subglobose, 30–35 mm in diameter, the sepals accrescent and subtending the fruits; seeds black, densely short tomentose.

This species flowers from November to March. It ranges through southern Florida, the West Indies, Mexico, Central America, South America and the Old World tropics.

BOCAS DEL TORO: Changuinola Valley, *Dunlap 546* (F, US). Water Valley, *Wedel 1698* (MO, US), *1793* (MO), *1816* (US), *1845* (MO, US). CANAL ZONE: Ancón, *Greenman & Greenman 5171* (MO). Balboa Heights, *Killip 3248* (US). Ancón, *Pittier 2754*. Balboa, *Standley 28552* (US). Near Fort Sherman, *Standley 31212* (US). COLÓN: Between France Field and Cativa1, *Standley 30397* (US). PANAMÁ: 5 mi. SW of Cerro Brewster, *Lewis et al. 3415* (MO).

5. **Merremia umbellata** (L.) Hall. f., Bot. Jahrb. (Syst.) 16: 552. 1893.—FIG. 6A, C.

Convolvulus umbellatus L., Sp. Pl. 155. 1753. TYPE: (not seen).

Ipomoea polyanthes Roem. & Schult., Syst. Veg. 4: 234. 1819. TYPE: Based on *Convolvulus umbellatus* L.

I. portobellensis Beurl., Kong. Vet. Handl. 139. 1854. TYPE: Panama, Portobelo, *Billberg 255* (S, not seen).—Placed in synonymy here by O'Donell (1960).

Vines; stems herbaceous, glabrate. *Leaves* entire, narrowly triangular to broadly ovate, mostly long-acuminate, basally truncate, cordate to hastate, densely pubescent to glabrous. *Flowers* in umbelliform inflorescences; sepals oblong, 6–8 mm long, rounded apically, the margins scarious, glabrous or pubescent; corollas yellow, 3–3.5 cm long. *Fruits* capsular, 8 mm in diameter; seeds dark brown, densely pubescent with short trichomes.

This species probably flowers all year; specimens have been seen from October to July. It occurs in southern Florida, the West Indies, Mexico, Central America, South America and in the Old World tropics.

BOCAS DEL TORO: Sta. Catalina, *Blackwell et al. 2721* (MO). Changuinola Valley, *Dunlap 355* (F, US). Hillside above Almirante, *Gentry 2816* (MO). Changuinola to 5 mi. S, *Lewis et al. 837* (MO). Water Valley, *Wedel 1858* (MO, US). CANAL ZONE: Between Miraflores and Panamá, *Blum 2071* (MO). Fort Sherman, *Burch et al. 1011* (MO). Frijoles, *Croat 8050* (MO). Boy Scout Road, *Croat 8964* (MO). Valley of Río Puente, *Dodge & Allen 17314* (MO); *Epplesheimer, 1910* (F). Chagres, *Fendler 241* (MO, US). Fort Kobbe along road to Venado Beach, *Gentry 2863* (MO). Gamboa, *Greenman & Greenman 5165* (MO). Between Gamboa and Darién Station, *Bro. Heriberto 99* (US). Between Farfan Beach and Palo Seco, *Hunter & Allen 447* (MO, US). Pipeline Road, *Kennedy 3069* (MO). Paraíso, *Killip 3345* (US), Ancón Hill, *Killip 3427* (US). Ancón, *Mason 3* (US). Cocoli Road, *Lewis et al. 777* (MO). Empire to Mandinga, *Piper 5442, 5506, 5533* (all US). Near Gatuncillo, *Piper 5622* (US). Around Culebra, *Pittier 2230* (US). Between Miraflores and Corozal, *Pittier 2498* (F, US). Fort San Lorenzo, *Porter et al. 5011* (MO). Barro Colorado Island, *Shattuck 576*

(F). Summit, *Standley 26953* (US). Near Gatún, *Standley 27272* (US). Gamboa, *Standley 28342* (US). Las Cascadas Plantation, *Standley 29531* (US). Darién Station, *Standley 31649* (US). Quebrada Melgada, Chagres River, *Steyermark 17468* (MO). Gatún, *Tyson 3516* (MO). Fort San Lorenzo, *Tyson & Blum 3695* (MO). Barro Colorado Island, *Wetmore & Abbe 185* (F); *Woodworth et al. 685* (F). Frijoles, *Woodworth & Vestal 721* (F). CHIRIQUÍ: Quebrada Melliza, 6 mi. S of Puerto Armuelles, *Leisner 429* (MO). COCLÉ: Foot of Cerro Pilón, *Porter et al. 4599* (MO). El Cope, *Tyson 5204* (MO). COLÓN: Above Gamboa, *Allen 4107* (MO). Near Peluca, along Río Boqueron, *Kennedy 2809* (MO). Around Portobelo, *Pittier 2471* (F, US). DARIÉN: Near Pinogana, *Allen 4288* (MO). El Real, *Burch et al. 1058* (MO). NE of Nurrá, *Duke 10082* (MO). Ca. 4 mi. above Santa Fé, *Duke 10213* (MO). Isla Casaya, *Duke 10384* (MO). Isla Pedro Gonzales, *Duke 10399* (MO). Without locality, *Macbride 2715* (F, US). Near Yaviza, *Stern et al. 168* (MO). Chepigana, *Terry & Terry 1370* (F, MO). HERRERA: La Avena to Pesé, *Burch et al. 1297* (MO). Chitré to Davisa, *Burch et al. 1363* (MO). 10 mi. S of Ocú, *Tyson et al. 2837* (MO). S of Carreta, *Burch et al. 1225, 1231* (both MO). PANAMÁ: Las Delicias, *Carleton 60* (US). Between Panamá and Chepo, *Hunter et al. 16628* (MO). Between Río Pacora and Chepo, *Dwyer et al. 5118* (MO). Old Panama City, *Greenman & Greenman 5146* (MO). Punta Paitilla, *Bro. Heriberto 223* (US). Near Chepo, *Hunter & Allen 30* (MO). San José Island, *Johnston 810* (MO, US). Near Abalaba, *Killip 3353* (US). Taboguilla Island, *Miller 1988* (US). Near Panamá, *Standley 26860* (US). Taboga Island, *Standley 27962* (US). Río Tocumen, *Standley 29457* (US). El Capitano, *Tyson 5360* (MO). SAN BLAS: Near Ailigandi, *Lewis et al. 193* (MO).

7. OPERCULINA

Operculina S. Manso, Enum. Subst. Bras. 16. 1836. TYPE: *O. convolvulus* S. Manso.

Lianas to small herbaceous vines, the stems, petioles, and pedicels often winged. *Leaves* entire to lobed, often cordate. *Flowers* axillary, in few-flowered cymes or solitary; sepals large, glabrous, enlarging in fruit and becoming coriaceous, often irregularly erose on the margins; corolla large, broadly campanulate, funnelform, or salverform, white, yellow, or reddish; stamens included, the anthers twisted at least in age, the pollen 3-colpate; ovary glabrous, bilocular, each locule bi-ovulate, the style included, filiform, the stigma biglobose. *Fruits* dehiscent at or above the middle by a circumscissile epicarp, the upper part more or less fleshy and separating from the lower part and from the endocarp, 2-locular, 4-seeded; the seeds glabrous or pubescent.

A tropical genus of 15–20 species. House (1906) did the last critical study of the North American species. Many of the species included by House are now placed in *Merremia*.

Literature:

House, H. D. Studies in the North American Convolvulaceae II. The genus *Operculina*. Bull. Torrey Bot. Club 33: 495–503. 1906.

a. Peduncles and sometimes stems conspicuously winged; corollas yellow ..... 3. *O. triquetra*
aa. Peduncles and stems without wings; corollas white, pink to red.

→

FIGURE 7. *Operculina*.—A. *O. triquetra* (Vahl) Macbr., habit (× 3/5).—B. *O. codonantha* (Benth.) Hall. f., fruiting stem section with leaf (× 3/5). [A after *Standley 26092* (US). B after *Wetmore & Abbe 246* (F).]

A
B
W. van Montfrans

b. Leaves 3–8 cm long; sepals to 2.5 cm long; corollas to 7 cm long, pink to red ..... 2. *O. pteripes*

bb. Leaves 8–15 cm long, sepals 2.5–3 cm long; corolla to 9 cm long, white or lilac ..... 1. *O. codonantha*

1. **Operculina codonantha** (Benth.) Hall. f., Bot. Jahrb. (Syst.) 16: 550. 1893.—FIG. 7B.

Ipomoea codonantha Benth., Pl. Hartw. 120. 1843. TYPE: Ecuador, Guayaquil, *Hartweg 676* (BM, not seen).

Lianas; stems glabrous or at least glabrate. *Leaves* cordate-acuminate, 8–15 cm long, 3–5 angled basally or sinuate-lobed (Bentham), basally cordate, apically acuminate, glabrous. *Flowers* solitary on elongate peduncles; sepals obovate, 2.5–3 cm long, obtuse, the outer sepals orbicular to broadly elliptic; corollas white or lilac, campanulate, to 9 cm long. *Fruits* operculate-capsular, depressed-globose, 3–3.5 cm in diameter, subtended by the accrescent calyx; seeds black, glabrous.

Operculina codonantha occurs in Peru, Ecuador and Panama.

This is a poorly known species. It is well distinct from *O. pteripes* in leaf shape. Fruiting specimens look much like *Merremia discoidesperma*, but the 2 species may easily be distinguished. Fruits of *O. codonantha* have a thickened basal portion, while those of *M. discoidesperma* are thin and papery throughout. Further, the seeds of *M. discoidesperma* are pubescent with short trichomes; those of *O. codonantha* are glabrous.

CANAL ZONE: Barro Colorado Island, *Wetmore & Abbe 246* (F). Frijoles, *Woodworth & Vestal 684* (F).

2. **Operculina pteripes** (G. Don) O'Donell, Lilloa 23: 435. 1950.

Calonyction pteripes G. Don, Gen. Syst. 4: 264. 1838. TYPE: Ecuador, herb. *Ruiz & Pavon*, (not seen).
Ipomoea alatipes Hook., Bot. Mag. 88: *t. 5330*. 1862. SYNTYPES: *Hayes, Seemann* and *Fendler 2084* (none seen).
I. pterodes sensu Seem., Bot. Voy. Herald 171. 1854, non Choisy (1845).
Operculina alatipes (Hook.) House, Bull. Torrey Bot. Club 33: 499. 1906.
O. pteropus Meisn. *in* Mart., Fl. Bras. 7: 214. 1869. TYPE: Ecuador, Guayaquil, *Pavon*, (not seen).

Vines; stems herbaceous at least toward the tips, glabrous. *Leaves* ovate, 3–8 cm long, acuminate, cordate basally, entire. *Flowers* in 2–7-flowered inflorescences, the peduncles smooth or rarely narrowly winged; sepals oblong, 2.5 cm long, acute to obtuse; corollas red-pink, subsalverform, 6–7 cm long. *Fruits* not seen.

Operculina pteripes flowers from November to December. It ranges from Mexico to Panama, Colombia and Peru.

While this species occasionally has slightly winged peduncles, the raised areas are not as pronounced as in *O. triquetra*. These species also differ in flower shape and color: campanulate and yellow in *O. triquetra*, salverform and pink to red in *O. pteripes*. They are often difficult to separate in fruit.

CANAL ZONE: Road to observation point SW of Thatcher Ferry Bridge, *Gentry* 2858 (MO). COCLÉ: W of Antón at Río Chico, *Tyson & Blum* 2589 (MO). HERRERA: La Avena to Pesé, *Burch et al. 1274* (MO). PANAMÁ: Matías Hernández, *Pittier 6868* (US). Near Santiago, *Allen 1011* (F).

3. **Operculina triquetra** (Vahl) Hall. f., Bot. Jahrb. (Syst.) 18: 120. 1894; Macbr., Field Mus. Nat. Hist., Bot. Ser. 13(5/1): 480. 1959, superfluous.—FIG. 7A.

Convolvulus triqueter Vahl., Symb., Bot. 3: 30. 1793. TYPE: St. Croix, *West*, herb. Vahl (C, not seen, IDC 2200-1, 14I 1.).
C. alatus Ham., Prodr. Fl. Ind. Occ. 24. 1824. TYPE: (not seen).
Ipomoea hamiltoni G. Don, Gen. Syst. 4: 268. 1838. TYPE: Tobago, *Hamilton* (not seen).
I. pterodes Choisy *in* DC., Prodr. 9: 361. 1845. TYPE: French Guiana, Cayenne, *Gabriel* (not seen).
I. altissima Mart. *ex* Choisy *in* DC., Prodr. 9: 359. 1845. SYNTYPES: Brazil, *Martius* (not seen).
Operculina alata (Ham.) Urb., Symb. Ant. 3: 343. 1902.

Vines; stems herbaceous, basally suffrutescent, glabrous. *Leaves* cordate-ovate to cordate-oblong, mostly 3-lobed, the 2–4 smaller basal lobes rounded or oblong, the middle lobe oblong, acuminate, 5–13 cm long, glabrous or glabrate. *Flowers* mostly solitary or dichasial, the inflorescences about equal to the leaf in length; sepals ovate to broadly ovate, 2.5–3 cm long, acute to obtuse, glabrous; corollas yellow, broadly campanulate, 4–6 cm long. *Fruits* depressed-globose, operculate-capsular, mostly 2 cm in diameter, subtended and mostly enclosed by sepals; seeds black, glabrous.

This species flowers from November to January. It ranges from the West Indies and Panama to Brazil and Peru.

CANAL ZONE: Albrook Tower, *Blum 2048* (MO). Between Miraflores and Panamá, *Blum 2068* (MO). Farfan Beach near Palo Seco, *Burch et al. 1412* (MO). Near Summit Garden, *Correa & Dressler 657* (MO). Roadside near Paraíso, *Croat 12783* (MO). Cocoli, *Dwyer 7206* (MO). SW of Thatcher Ferry Bridge, *Gentry 2859* (MO). E of Curundu, *Harvey 5203* (F). Near Madden Dam, *Lewis et al. 30* (MO). Balboa, *Standley 25514* (MO, US), *26092* (US). Between Fort Clayton and Corozal, *Standley 29127* (US). Near Summit, *Standley 30121* (US). PANAMÁ: Without locality, *Allen 1128* (MO); *Kennedy 2078* (MO). Taboga Island, *Macbride 2805* (F, US). Matías Hernández, *Pittier 6888* (US). Río Tocumen, *Standley 29450* (US). Between Matías Hernández and Juan Díaz, *Standley 32076* (US). VERAGUAS: Mouth of Río Concepción, *Lewis et al. 2870* (MO).

8. ANISEIA

Aniseia Choisy, Mém. Soc. Phys. Genève 6: 481. 1833. LECTOYPE: not chosen.

Herbaceous *vines*. *Leaves* linear to ovate or elliptic, often mucronate, entire. *Flowers* axillary, solitary or in few-flowered dichasia; sepals 5, herbaceous, unequal, the 3 outer sepals larger, often decurrent on the pedicel; corolla white, broadly funnelform, the limb 5-dentate or sub-entire with 5 pubescent interplicae; stamens and style included, the pollen pantocolpate; ovary glabrous, 2-locular, the locules bi-ovulate; the disc small or absent; style 1, slender, the stigma bi-globose. *Fruits* capsular, globose, 2-celled, 4-valvate; seeds 4, glabrous.

The genus contains about 5 American species, one of which extends into the Old World tropics. There is only one species in Panama.

FIGURE 8. *Aniseia martinicensis* (Jacq.) Choisy.—A. Habit (× ½).—B. Fruit (× 1). [A after *Oliver et al.* 3535 (MO). B after *Burch et al. 1360* (MO).]

1. **Aniseia martinicensis** (Jacq.) Choisy, Mém. Soc. Phys. Genève 8: 144. 1839.—FIG. 8.

Convolvulus martinicensis Jacq., Sel. Stirp. Amer. 26, *t. 17*. 1763. TYPE: *Jacquin* (not seen).
C. uniflorus Burm. f., Fl. Indica 47, 5. 21, *f. 2*. 1768. TYPE: Java (not seen).
Aniseia uniflora (Burm. f.) Choisy, Mém. Soc. Phys. Genève 6: 483. 1833.
Ipomoea lanceolata G. Don, Gen. Syst. 4: 282. 1837. TYPE: Sierra Leone (not seen).

Vines; stems herbaceous, at least above, glabrous to sparsely pubescent. *Leaves* narrowly lanceolate, 4–8 cm long, obtuse to acute basally, obtuse and mucronate apically, entire, glabrate. *Flowers* mostly solitary in the leaf axils, peduncles to 5 cm long; sepals broadly ovate, the outer 2 broader than the inner 3, 12–17 mm long, acuminate; corollas white, campanulate, 25–30 mm long. *Fruits* capsular, ovoid, ca. 2 cm long, subtended by the enlarged calyx; seeds black, glabrous.

Aniseia martinicensis probably flowers all year, and specimens have been taken from September to July. It ranges from southern Florida and the Antilles to Panama and South America.

This species is easily distinguished by the white corollas associated with broadly ovate sepals that grade in size. It prefers moist habitats such as swamps and marshes.

CANAL ZONE: Barro Colorado Island, *Bailey 674* (F); *Bangham 589* (F); *Brown 52* (F); *Croat 4201* (F). Albrook, *Dwyer 6534* (MO). Barro Colorado Island, *Ebinger 579* (MO). Chagres, *Fendler 237* (F, US). Between Frijoles and Monte Lirio, *Killip 12182* (US). Barro Colorado Island, *Shattuck 442* (F, MO); *Wetmore & Abbe 216* (F, MO); *Woodworth & Vestal 455, 704* (both F, MO). HERRERA: Chitré to Davisa, *Burch et al. 1360* (MO). LOS SANTOS: Between Tonosí and Macaracas, *Oliver et al. 3535* (MO). PANAMÁ: Matías Hernández, *Pittier 6937* (US).

5. IPOMOEEAE

Ipomoeeae Hall. f., Bot. Jahrb. (Syst.) 16: 358. 1893. TYPE: *Ipomoea* L.

9. IPOMOEA

Ipomoea L., Sp. Pl. 159. 1753; Gen. Pl., ed. 5, 76. 1754. LECTOTYPE: *I. pes-tigridis* L.

Quamoclit Moench, Meth. Bot. 453. 1794. LECTOTYPE: *Ipomoea coccinea* L.
Batatas Choisy, Mém. Soc. Phys. Genève 6: 434. 1833. LECTOTYPE: *B. edulis* Choisy = *Ipomoea batatas* (L.) Poir.
Pharbitis Choisy, Mém. Soc. Phys. Genève 6: 438. 1833. LECTOTYPE: *P. hispida* Choisy = *Ipomoea purpurea* (L.) Roth.
Calonyction Choisy, Mém. Soc. Phys. Genève 6: 441. 1833. LECTOTYPE: *C. speciosum* Choisy = *Ipomoea alba* L.
Exogonium Choisy, Mém. Soc. Phys. Genève 6: 443. 1833. LECTOTYPE: *Ipomoea bracteata* Cav.

Vines, shrubs or trees, usually twining, sometimes prostrate or floating. *Leaves* mostly petiolate, often variable in shape and size on the same plant, entire, lobed, divided, or rarely compound, the petiole occasionally with pseudostipules. *Flowers* mostly in axillary 1- to many-flowered dichasia, rarely paniculate; sepals herbaceous or subcoriaceous, variable in size and shape, glabrous or pubescent, often somewhat enlarged in fruit; corolla small to large, regular, or rarely slightly zygomorphic, mostly funnelform or campanulate, less often tubular or salverform, purple, red, pink, white, or yellow, the limb shallowly or rarely deeply lobed, the interplicae well defined by 2 distinct nerves; stamens included or rarely exserted, the filaments filiform, often triangular-dilated at the base, mostly unequal in length; the pollen pantoporate, globose, spinulose; ovary usually 2- or

sometimes 4-locular, 4-ovulate, rarely 3-locular, 6-ovulate, glabrous or pubescent, the style simple, filiform, included or rarely exserted, the stigma capitate, entire or often 2(–3)-globose. *Fruits* globose or ovoid capsules, mostly 4(–6)-valved or rarely splitting irregularly; seeds 4, (6, or less), glabrous or pubescent.

This is the largest genus-complex in the family with about 500 species widely distributed in the tropics and subtropics of both hemispheres. The species-groups here included in *Ipomoea* have been recognized as genera, subgenera, and sections. Evidence suggests that some of these species-groups may be natural, while others are certainly polyphyletic. Convergent evolution in several characters appears to account for part of the difficulty in delimiting natural taxa, *e.g. Quamoclit* and *Exogonium* both have flowers adapted for hummingbird pollination; *Quamoclit* seems to be monophyletic, while *Exogonium* is polyphyletic. Part of *Exogonim* probably has its closest alliance with the *Pharbitis* species. Much study is needed to determine relationships and, in spite of obscuring some apparent relationships, it seems best to consider the group in the broad sense at this time.

Two revisions of *Ipomoea* consider the species-groups in a restricted sense, House (1908) and Matuda (1964–1965). One of these treatments is limited by its age, the other by geographic range. O'Donell (1959) updated House's previous (1909) treatment of *Quamoclit*, and his study indicates the naturalness of the group. The species relegated to *Calonyction* have been studied by Gunn (1972). Gunn's study and our study of the species (Austin & Conroy, unpublished data) indicate that this taxon is unnatural.

As has been pointed out by Standley and Williams (1970), many species of *Ipomoea* range widely and a detailed comparison of North and South American species will probably result in more changes of present alignments.

There is documentation for 31 species in Panama.

Literature:

Gunn, C. R. Moonflowers, *Ipomoea* section *Calonyction*, in temperate North America. Brittonia 24: 150–168. 1972.

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Matuda, E. El genero *Ipomoea* en Mexico. Ann. Inst. Biol. 24: 85–145; 25: 45–47; 26: 83–106. 1964–1965.

O'Donell, C. A. Las especies Americanas de *Ipomoea* L. sect. *Quamoclit* (Moench) Griseb. Lilloa 29: 19–86. 1959.

Standley, P. C. & L. O. Williams. Convolvulaceae. *In* "Flora of Guatemala." Fieldiana, Bot. 24(9): 4–85. 1970.

KEY TO *IPOMOEA* GROUPS

a. Corollas salverform, the long narrow tube only slightly widened near or above the middle (occasional exception in *I. purga*), abruptly flaring near summit; anthers exserted (except *I. macrantha*); either open during night and closing in early morning or open most of day.

b. Sepals and stems covered with large fleshy trichome-like structures (*I. setosa*) ..... Group 4. *Eriospermum*

bb. Sepals glabrous or slightly puberulent.

c. Corolla tube 6–14 cm long, the limb and tube white or partially green; flowers open during night and closing in early morning ..... Group 6. *Calonyction*

cc. Corolla tube 2–8 cm long, the limb and tube red-purple, red to orange or yellow (white in a cultivar of *I. quamoclit*); flowers open during mornings or all day.

d. Corolla 2–3.5 cm long, red to orange or yellow (rarely white); sepals with abruptly constricted, long fleshy-caudate apices or mucronate ..... Group 8. *Quamoclit*

dd. Corolla 6–8 cm long, lavender to red-purple; sepals apically obtuse and cuspidate ..... Group 7. *Exogonium*

aa. Corolla funnelform to campanulate, the short to long tubes expanding from below the middle, gradually or abruptly flaring near summit; anthers mostly included; open during morning, closing near noon.

e. Glabrous perennials with procumbent stems, not normally twining; habitat of coastal dunes and beaches or inland waterway margins; leaves fleshy or leathery; sepals elliptic-oblong to orbicular ..... Group 3. *Erpipomoea*

ee. Glabrous or pubescent annuals or perennials with twining or erect stems, not normally rooting at nodes (except in cultivated forms of *I. batatas*); habitat various; leaves chartaceous to fleshy; sepals acuminate to suborbicular.

f. Sepals herbaceous; sepals, peduncles or pedicels with reflexed or erect trichomes (except *I. acuminata*); stigma lobes 3 and the ovary 3–4-locular, each locule bi-ovulate; corollas blue, red, or white ..... Group 1. *Pharbitis*

ff. Sepals coriaceous or membranaceous, rarely herbaceous; sepals, peduncles and pedicels glabrous or at least without reflexed trichomes; stigma lobes 2 and the ovary 2(–3)-locular, each locule uniovulate; corollas mostly lavender, sometimes blue or white.

g. Sepals mostly coriaceous; large, perennial vines or shrubs; seeds oblong, comose at least on margins; corollas mostly large and funnelform ..... Group 4. *Eriospermum*

gg. Sepals membranaceous to chartaceous; smaller annual or perennial vines; seeds suborbicular or pyriform, mostly glabrous, if pubescent not comose; corollas small to large, funnelform to campanulate.

h. Leaves pedately dissected ..... Group 5. *Orthipomoea*

hh. Leaves entire-cordate to shallowly 3- or 5-lobed but not pedately dissected.

i. Sepals with prominent white or pale scarious or subscarious margins, the outer sepals to ½ or ⅔ as long as the inner, apex acute to rounded, non-apiculate; seeds pyriform ..... Group 5. *Orthipomoea*

ii. Sepals without prominent white or pale scarious or subscarious margins, the outer sepals mostly about the same length as the inner (outer sepals shorter in *I. trifida*), apex acute to acuminate, apiculate to mucronate; seeds suborbicular ..... Group 2. *Batatas*

Group 1. PHARBITIS

Pharbitis Choisy, Mém. Soc. Phys. Genève 6: 438. 1833. TYPE: *I. purpurea* (L.) Roth.
Ipomoea sect. *Pharbitis* (Choisy) Griseb., Fl. Brit. W. Ind. 473. 1864.
I. subg. *Pharbitis* (Choisy) Clarke, Fl. Brit. India 4: 199. 1883.

a. Sepals glabrous or soft-pubescent outside with slender trichomes.

b. Foliaceous bracts at the bases of the pedicels; sepals minutely aculeolate along the costa ..... 5. *I. setifera*

bb. Squamiform bracts at the bases of the pedicels; sepals smooth to appressed pubescent along the costa ..... 1. *I. acuminata*

aa. Sepals hispid-pilose outside with long spreading trichomes.

c. Corollas 2–3 cm long; inflorescences dense and capitate ..... 2. *I. meyeri*

cc. Corollas 4–8 cm long; inflorescences open.

d. Sepals with slightly narrowed green tips shorter to slightly longer than the body ---- 4. *I. purpurea*
dd. Sepals with very narrow elongate green tips much longer than the body.
e. Sepals abruptly narrowed, the long subacute tips strongly spreading or curved ---- *I. hederacea*
ee. Sepals gradually narrowed, the long acute tips suberect, straight, scarcely spreading ---- 3. *I. nil*

1. **Ipomoea acuminata** (Vahl) Roem. & Schult., Syst. Veg. 4. 228. 1819, non Ruiz & Pavon, Fl. Peru 2, *t. 120*. 1799, nomen nudum.

Convolvulus acuminatus Vahl, Symb. Bot. 3: 26. 1794. TYPE: St. Croix, *West* (not seen).
Ipomoea congesta R. Br., Fl. Nov. Holl., ed. 1. 485. 1810. TYPE: Australia, Queensland, *Banks & Solander* (BM, not seen).
I. cathartica Poir. *in* Lam., Encycl. Méth. Suppl. 4: 633. 1816. TYPE: St. Domingo, *Poiteau* (P-JU-6829, not seen).
I. vahliana House, Ann. New York Acad. Sci. 18: 204. 1908. Nom. nov. for *Convolvulus acuminatus* Vahl.
I. indica (Burm.) Merrill, Int. Rumph. Herb. Amb. 445. 1917.
Convolvulus indicus Burm., Ind. Univ. Herb. Amb. 7. 1755. TYPE: Rumphius, Java (not seen).

Vines; stems twining, much branched, herbaceous to somewhat woody near the base, perennial, the stems appressed-pubescent to glabrate. *Leaves* rounded-ovate, commonly with 3 lobes, 5–9 cm long, basally cordate, apically acuminate, densely pubescent to glabrate. *Flowers* in 1- to few-flowered cymes, the cymes usually silky white-pubescent; sepals lanceolate to ovate to broadly-ovate, 10–20 mm long, apically acuminate to long-acuminate, appressed pubescent to glabrate; corolla blue or purple, rarely white, 5–7 cm long, the limb 6–8 cm broad. *Fruits* capsular, to 1 cm broad, globose to somewhat apically flattened depending on the number of seeds developing, glabrous; seeds commonly 4, tan to dark brown, glabrous.

The name *I. indica* (Burm.) Merrill (Int. Rumph. Herb. Amb. 445. 1917) based on *Convolvulus indicus* Burm. (Ind. Univ. Herb. Amb. 7. 1755) has priority over the name used here, but does not clearly refer to the same species.

This pantropical species flowers throughout the year. "Batatilla."

BOCAS DEL TORO: Bocas del Toro Island airport, *Lewis et al. 782* (MO). S of mouth of Changuinola River, *Lewis et al. 873* (MO). Changuinola Valley, *Dunlap 569* (F, US). Near Chiriquí Lagoon, *Wedel 2450* (MO), *2606* (MO, US). Isla Colón, *Wedel 2956* (MO, US). Snapper Point, *Wedel 2640* (US). SW of Bocas, *Wedel 541* (MO). CANAL ZONE: Near Fort Sherman, *Standley 31189* (US). Between Gorgona and Mamei, *Pittier 2242* (F, US). Gamboa, *Heriberto 109* (US). Laguna near Vera Cruz, *Greenman 48* (F). CHIRIQUÍ: Distrito Baru along ridge above Brazo Seco, *Croat 22550* (MO). COLÓN: 1 mi. SW of Portobelo, *Croat 11371* (MO). Nuevo Chagres, *Lewis et al. 1859* (MO). Portobelo, *Dwyer 4355* (MO). DARIÉN: Headwaters of Río Chico, *Allen 4637* (MO). PANAMÁ: Bella Vista, *Standley 25300* (US); *Killip 12002* (US). Las Delicias, *Carleton 231* (US). Panamá Viejo, *Dodge 17521* (MO); *Mendez 136* (MO). Río Pacora near confluence with Río Corso, *Duke 12035* (MO). Sabanas, *Bro. Paul 623, 624* (both US). Taboga Island, *Miller 1943* (US); *Tyson & Loftin 5132* (MO). SAN BLAS: Near Puerto Obaldía, *Croat 16872, 16887* (both MO). Mouth of Aligandi River, *Lewis et al. 208* (MO). Airport at Irandí, *Duke 6517* (MO).

2. **Ipomoea meyeri** (Spreng.) G. Don, Gen. Syst. 4: 275. 1838.

Convolvulus meyeri Spreng., Syst. Veg. 1: 597. 1825. TYPE: ?*Meyer* (not seen).
Ipomoea chiapensis Brandeg., Univ. California Publ. Bot. 6: 60. 1914. TYPE: Mexico, Tonala, *Purpus 6907* (MO).

I. brachypoda Benth., Bot. Voy. Sulph. 135. 1844. TYPE: (not seen).

Vines; stems small, slender and herbaceous, glabrous to somewhat pubescent. *Leaves* broadly ovate, 4–10 cm long, entire or hastate-trilobate, basally cordate, apically acute to acuminate, glabrate. *Flowers* in few- to several-flowered cymose clusters on peduncles about as long as the petiole; sepals long-lanceolate, 10–20 mm long, apically linear-lanceolate, pilose to hirsute with spreading trichomes; corolla blue to purplish with a white throat, 2–3 cm long. *Fruits* capsular, globose, 8 mm in diameter; seeds densely pubescent with short trichomes.

This species flowers from November to February. It ranges through the West Indies and southern Mexico to Panama and northern South America.

CANAL ZONE: Along Las Cruces Trail, *Hunter & Allen 676* (MO). Around El Paraíso, *Pittier 2533* (US). Balboa, *Standley 25527, 25547* (both US). Near Summit, *Standley 25804* (US). Between Fort Clayton and Corozal, *Standley 29117* (US). Balboa, *Standley 32127* (US). HERRERA: Near Ocú, *Allen 4073* (MO). PANAMÁ: Punta Paitilla, *Piper 5425* (US). Las Sabanas, *Standley 25880* (US). Along Corozal Road, *Standley 26772* (US). Near Juan Franco Race Track, *Standley 27687* (US). Taboga Island, *Standley 27855* (US). Near Matías Hernández, *Standley 28925* (US). Tumba Muerto Road, *Standley 29714* (US). Juan Díaz, *Standley 30504* (US). CHIRIQUÍ: Distrito Guanabano, along Quebrada Quanabano, *Croat 22542* (MO). VERAGUAS: Vicinity of Santiago, *Allen 1085* (MO).

3. **Ipomoea nil** (L.) Roth, Cat. 1: 36. 1797.

Convolvulus nil L., Sp. Pl., ed. 2. 219. 1762. LECTOTYPE: U.S.A., illustration of *Convolvulus caeruleus hederaceo folio magis anguloso* Dill., Hort. Elth. *t. 80, fig. 92.* 1732.

Vines with large trichomes, annual, densely to scattered pubescent throughout. *Leaves* ovate to suborbicular, 5–15 cm long, entire or 3(–5)-lobed, basally cordate, the lobes apically acute to acuminate, pubescent. *Flowers* in 1–5-flowered, often dense cymose clusters of mature and developing buds and flowers, sepals long-lanceolate, 15–25 mm long, with linear-lanceolate apices, densely long-hirsute; corolla blue, purple or almost scarlet, throat often white, 3–5 cm long, the limb 4–5 cm broad. *Fruits* capsular, subglobose to globose, 8–12 mm in diameter; seeds pyriform, densely pubescent with short trichomes.

Ipomoea nil flowers from December to July. It is pantropical in distribution.

This widely cultivated and variable species is often confused with *Ipomoea purpurea*, *I. acuminata*, or *I. hederacea*. *Ipomoea acuminata* may be separated by its wide and less herbaceous sepals and *I. purpurea* by its acute to obtuse sepals. There is much less difference between *I. nil* and *I. hederacea*. The best way to distinguish them is that the sepals of *I. nil* are gradually narrowed with the long acute tips suberect, straight, and scarcely spreading. The sepals are more abruptly narrowed and spreading or curved in *I. hederacea*. I am not fully convinced that these 2 names represent more than one variable species.

CANAL ZONE: Managre Beach, *Tyson et al. 2887* (MO). PANAMÁ: San José Island, *Erlanson 476* (US); *Johnston 945* (MO). LOS SANTOS: Chitré to Las Tablas, *Burch et al. 1214* (MO).

4. **Ipomoea purpurea** (L.) Roth, Bot. Abh. 27. 1787.

Convolvulus purpurea L., Sp. Pl., ed. 2. 219. 1762. LECTOTYPE: U.S.A., illustration of *Convolvulus folio cordato glabro flore violaceo* Dill., Hort. Elth. *t. 84, fig. 97.* 1732.

Pharbitis diversifolius Lindley, Bot. Reg. 23: *t. 1988*. 1837. TYPE: Not seen. Lindley's plate is a good illustration of the species treated here.
Ipomoea purpurea var. *diversifolia* (Lindley) O'Donell, Lilloa 26: 385. 1953.

Vines; stems slender and herbaceous, annual, pilose or hirsute with spreading trichomes. *Leaves* broadly ovate to cordate, 2–10 cm long, entire or trilobate, pubescent on both surfaces. *Flowers* in 1–5-flowered cymose clusters on peduncles usually longer than the petioles; sepals oblong-lanceolate, 8–16 mm long, apically abruptly acute, hirsute on the basal portion; corolla blue, purple, pink, or with stripes of these colors on a white background, throat white, 3–5 cm long. *Fruits* capsular, depressed-globose, 10 mm in diameter; seeds black, pyriform, glabrous.

The species flowers in June. It is pantropical but native to the Americas.

Ipomoea purpurea is distinguished from *I. nil* by the abruptly acute to obtuse sepals; they are lanceolate and elongate in *I. nil*.

CHIRIQUÍ: Bambito, 1 mi. SW of Cerro Punta, *Tyson 5662* (MO).

5. **Ipomoea setifera** Poir. *in* Lam., Encycl. Méth. 6: 17. 1804. TYPE: Guyana, *Brocheton* (not seen).

Convolvulus ruber Vahl, Eclog. 2: 12. 1789. TYPE: (not seen).
Ipomoea rubra (Vahl) Millsp., Field Mus. Bot. 2: 86. 1900, *non* Murray (1791).

Vines; stems twining, herbaceous, hirsute with mostly erect trichomes, also sometimes minutely aculeolate. *Leaves* broadly ovate-cordate to triangular-hastate, 7–14 cm long, the basal lobes obtuse to acute, apically acute to obtuse, glabrous. *Inflorescences* 5–7-flowered, cymose, with foliaceous bracts at the base of the pedicels. *Flowers* rose to purple; sepals unequal, the outer 3 broadly ovate, 15 mm long, obtuse to subacute, mucronate, the inner 2 ovate-lanceolate, 12 mm long, acute to acuminate, glabrous but aculeolate along the costa; corolla 6–7 cm long, the limb 4–5 cm wide. *Fruits* not seen.

This species flowers in February. It occurs in Guatemala, British Honduras, Nicaragua, Costa Rica, Panama, South America, the West Indies and in tropical Africa.

Hemsley (Biol. Centr. Amer. Bot. 2: 394. 1882) reported a collection of this species from Chagres (*Fendler*) that I have not seen. There has been a recent collection from near the Costa Rica-Panama border (Puntarenas Province, Costa Rica, *Liesner 256* MO). The species will probably be found at more sites in Panama.

Group 2. BATATAS

Batatas Choisy, Mém. Soc. Phys. Genève 6: 434. 1833. TYPE: *I. batatas* (L.) Poir. *in* Lam.
Ipomoea sect. *Batatas* (Choisy) Griseb., Fl. Brit. W. Ind. 468. 1864.
I. subg. *Batatas* (Choisy) Clarke, Fl. Brit. India 4: 201. 1883.

a. Outer sepal apex acute to obtuse, sepals glabrous ..... 7. *I. tiliacea*
aa. Outer sepal apex acute or acuminate and awned, sepals pubescent or at least ciliate.
  b. Outer sepals ovate, apically acute, awned; the back either glabrous or less commonly puberulent, often ciliate ..... 8. *I. trifida*

bb. Outer sepals oblong to obovate, apex acuminate and awned; the back usually pubescent, often ciliate, rarely glabrous ..... 6. *I. batatas*

6. **Ipomoea batatas** (L.) Poir. *in* Lam., Encyl. Méth. 6: 14. 1804.

Convolvulus batatas L., Sp. Pl. 154. 1753. TYPE: Linn herb. (LINN 218.12, not seen, microfiche).
Ipomoea triloba auct. non L.
I. davidsoniae Standl., Publ. Field Mus. Nat. Hist., Bot. Ser. 22: 98. 1940. TYPE: Panama, *Davidson 595* (F, holotype; MO, isotype).
I. mucronata Schery *in* Woods. & Schery, Ann. Missouri Bot. Gard. 28: 463. 1941. TYPE: Panama, *Woodson & Schery 283* (MO, lectotype).

Vines; stems usually somewhat succulent but sometimes slender and herbaceous; perennial, glabrous or pubescent. *Leaves* variable, from cordate to ovate, entire, dentate or often deeply lobed, 5–10 cm long, glabrous or rarely pubescent. *Flowers* absent in some varieties, frequent in others, in few-flowered cymose inflorescences; sepals oblong, the outer sepals acuminate and cuspidate, (8–)10–15 mm long, mostly pubescent or ciliate; corolla with a lavender to purple-lavender limb and darker throat, white in some varieties, 4–7 cm long. *Fruits* uncommonly formed, ovoid, glabrous; seeds rotund, glabrous.

Ipomoea batatas flowers from October to July. It is widely used as food and is pantropical through introductions by man.

Standley and other students of the Central American flora have confused the seed-grown plants of this species with others. The concept in virtually all of the American floras and monographs of the Convolvulaceae recognizes only the cultivated varieties of *I. batatas*. For further discussion see *I. trifida*. "Camote."

CANAL ZONE: Gamboa Dock, *Dwyer 6559* (MO). Gatun Station, *Hayes 586* (NY). Along Las Cruces Trail, *Hunter & Allen 677, 683, 687, 708* (all MO). Near Madden Dam, *Lewis et al. 43* (MO). Juan Mina, *Piper 5685* (US). Between Corozal and Ancón, *Pittier 2177* (US). N. of Gamboa, *Robyns 65-43* (MO). Balboa, *Standley 25632, 25638, 25639* (all US). Gamboa, *Standley 28343, 28439, 28455* (all US). Near E. Paraíso, *Standley 29935* (US). Balboa, *Standley 30895* (US). Darién Station, *Standley 31541, 31608* (both US). Obispo, *Standley 31666, 31733* (both US). CHIRIQUÍ: Near Bambito, *Croat 10617* (MO). Roadside between Cerro Punta and Bajo Grande, *Croat & Porter 16004* (MO). Bajo Mono, *Davidson 595* (F, MO). Near Boquete, *Lewis et al. 386* (MO). Around El Boquete, *Pittier 2909* (F, US). Near Camiseta, *Terry 1368* (F, MO). Near Tucutí, *Terry & Terry 1410* (F, MO). Finca Lerida to Peña Blanca, *Woodson & Schery 283, 323* (both MO). COCLÉ: Near El Valle, *Croat 13277* (MO); *Duke 12145* (MO). Cerro Pilón, *Lallathin 5041* (MO). El Valle de Antón, *Lewis et al. 2530* (MO). Boca del Toabré, *Lewis et al. 5485* (MO). Foot of Cerro Pilón, *Porter et al. 4602* (MO). COLÓN: Between France Field and Cativa1, *Standley 30361* (US). DARIÉN: Between Pinogana and Yavisa, *Allen 274* (F, MO). Above Río Venado, *Duke 9264* (MO). Río Pinas, *Duke 10557* (MO). Along Sambú River, *Pittier 5547* (US). PANAMÁ: Cerro Azul, *Croat 13020* (MO). Tocumen, *Dwyer 4883* (MO). Beyond Goofy Lake, *Dressler 572* (MO). Chimán, *Lewis et al. 3312* (MO). Near Cerro Jefe, *Lewis & Dressler 7549* (MO). Near Old Panama, *Bro. Paul 208* (US). Río Tocumen, *Standley 29458* (US). Juan Díaz, *Standley 30483* (US). Between Las Sabanas and Matías Hernández, *Standley 31884* (US). SAN BLAS: Outskirts of Puerto Obaldía, *Gentry 1566* (MO).

7. **Ipomoea tiliacea** (Willd.) Choisy *in* DC., Prodr. 9: 375. 1845.

Convolvulus tiliaceous Willd., Enum. Pl. 1: 203. 1809. TYPE: Herb. Willd. 3691 (B-W, not seen; IDC 7440 255I 1).
C. fastigatus Roxb., Hort. Beng. 13. 1814. TYPE: (not seen).
Ipomoea fastigata (Roxb.) Sweet, Hort. Brit. 288. 1826.

Vines; stems slender and herbaceous, lignescent especially near the base, probably a short-lived perennial, glabrous. *Leaves* ovate, 5–15 cm long, basally cordate, apically acuminate with an acute or obtuse mucronulate acumen, mostly entire, glabrous. *Flowers* in few- to several-flowered cymose groups terminating a peduncle that is often longer than the petiole; sepals ovate or the inner ovate-lanceolate, 5–10 mm long, apically acute, mucronulate, usually glabrous; corolla with a pink to lavender limb, the throat darker, 4–6 cm long. *Fruits* capsular, globose to depressed-globose, often 4-angled; seeds dark brown, rotund, glabrous.

Ipomoea tiliacea flowers from July to February. It occurs in southern Florida, the West Indies, Mexico, Central America and South America.

Usually this species is easily distinguished from others by the large acute sepals that dry brown. The 4-seeded and 4-lobed capsules are also distinctive.

BOCAS DEL TORO: Sta. Catalina, *Blackwell et al. 2755* (MO). Bocas del Toro, *Carleton 101* (US). Region of Almirante, *Cooper 182* (F). Along railroad at Milla, *Croat & Porter 16348* (MO). Vicinity of Almirante, *Croat 16501* (MO). Changuinola Valley, *Dunlap 260* (US). Changuinola, *Lewis et al. 813* (MO). Water Valley, *Wedel 830* (MO). Near Chiriquí Lagoon, *Wedel 1358, 1879* (both MO, US). Old Bank Island, *Wedel 1984* (MO, US). Johns Creek, *Wedel 2757* (MO, NY). Isla Colón, *Wedel 2984* (MO, US). CANAL ZONE: Barro Colorado Island, *Bailey 673* (F); *Brown 88, 174, 192* (all F). Mindi, *Cowell 170* (NY). Barro Colorado Island, *Croat 4620, 6869* (both MO, NY), *5633, 11946* (both MO). N of Escobal, *Croat 12433* (MO, NY). Gamboa, *Ebinger 491* (MO); *Greenman & Greenman 5159* (MO). Grounds of Fort Lorenzo, *Porter et al. 4998* (MO). Barro Colorado Island, *Shattuck 467, 714* (both F, MO). Near Summit, *Standley 29526* (US). Barro Colorado Island, *Starry 121, 266* (both F). Near Río Frijol, *Tyson 1480* (MO). Barro Colorado Island, *Wetmore & Abbe 159* (F); *Woodworth & Vestal 451, 499, 578* (all F). COCLÉ: Boca del Toabré, *Lewis et al. 5494* (MO). COLÓN: Mouth of Río Piedras, *Lewis et al. 3195* (MO). Between France Field and Cativa1, *Standley 30247* (US). SAN BLAS: Isla Oskatupo, *Duke 8513, 8933, 10189* (all MO). Mainland opposite Playon Chico, 0–3 mi. from Caribbean, *Gentry 6366* (MO); *Kirkbride 191A* (MO). Mainland opposite Ailigandi, *Lewis et al. 206* (MO). VERAGUAS: 5 mi. W of Santa Fé, *Croat 23237* (MO).

8. **Ipomoea trifida** (H.B.K.) G. Don, Gen. Syst. 4: 280. 1838.

Convolvulus trifidus H.B.K., Nov. Gen. Sp. Pl. 3: 107. 1819. TYPE: Venezuela, *Humboldt* (P, not seen).
Ipomoea ramoni auct. non Choisy (1845).
I. commutata auct. non Roem. & Schult. (1819).
I. trichocarpa auct. non Ell. (1817).

Perennial *vines*; stems very slender and delicate, finely pubescent. *Leaves* variable, cordate-ovate, entire to deeply 3- or 5-lobed. *Inflorescences* cymose, mostly with more than one flower open at a time. *Flowers* with the sepals unequal, the outer sepals 5–7 mm long, the inner sepals 10 mm long, apically acute, mucronate, finely pubescent or only ciliate, mostly drying to a straw color; corolla light lavender with a lavender-purple throat, 3–4 cm long. *Fruits* capsular, subglobose, 5–7 mm in diameter; seeds brown, rotund, glabrous.

Ipomoea trifida flowers from November to March. Its distribution is circum-Caribbean including Cuba; it is apparently introduced into Malaysia.

In his published works and annotations, Standley confused this species in most cases with two others. The majority of his determinations of these plants were as *I. triloba*; the remainder are plants of *I. batatas* grown from seed. Other

authors have made the same errors. After studying several hundred specimens and growing plants in this complex, I find that *I. triloba* has not been collected in Panama, Costa Rica or Guatemala. It has been collected only in Honduras, British Honduras and Mexico. The species is largely West Indian. *Ipomoea trifida*, however, is common from southern Mexico to northern South America. It is distinguished from other species in the complex by the shorter outer sepals which are ovate and usually dry straw-yellow. The complex will be examined in detail in a revision I now have in progress.

CANAL ZONE: S of El Valle de Antón, *Allen 2859* (F, MO). Madden Dam, *Dwyer 2876* (MO). Ancón Hill, *Greenman & Greenman 5134* (MO). Along Las Cruces Trail, *Hunter & Allen 723* (MO). Ancón Hill, *Killip 3286* (US). Without locality, *Macbride & Featherstone 2780* (MO). Around Frijoles, *Pittier 2677* (US). Balboa, *Standley 25521* (US). Sosa Hill, *Standley 25282* (US). Balboa, *Standley 26095* (US). Ancón Hill, *Standley 26335A* (US). Balboa, *Standley 26087, 27146, 29306, 32123* (all US). CHIRIQUÍ: 5.3 mi. N of David, *Lewis et al. 730* (MO). David, *Lewis et al. 757* (MO). COCLÉ: Río Hato, *Burch et al. 1142* (MO). HERRERA: Near Ocú, *Allen 4080* (MO). From Chitré to Divisa, *Burch et al. 1364* (MO). 4 mi. S of Los Pozos, *Tyson 2682* (MO). LOS SANTOS: 3 mi. S of Chitré, *Croat 9711* (MO). 5 mi. S of Pocrí, *Croat 9735* (MO). Between Tonosí and Macaracas, *Oliver et al. 3534* (MO). Between Tonosí and Guanico, *Stern et al. 1874* (US). PANAMÁ: Isla del Rey near San Miguel, *Duke 10429* (MO). Río Coronado along Pan American Highway, *Gentry 2905* (MO). Taboga Island, *Macbride 2780* (F, US). Sabanas, *Bro. Paul 151, 205* (both US). Matías Hernández, *Pittier 6934* (US). Las Sabanas, *Standley 25863* (US). Along Corozal Road, *Standley 26883* (US). Taboga Island, *Standley 27059* (US). Near Juan Franco Race Track, *Standley 27706* (US). Taboga Island, *Standley 27901* (US). Near Matías Hernández, *Standley 28869, 28951* (both US). Between Matías Hernández and Juan Díaz, *Standley 32073* (US). Río Mar, *Tyson et al. 2326* (SMU). 1 mi. W of Bejuco, *Tyson & Blum 2538* (US).

Group 3. ERPIPOMOEA

Ipomoea sect. *Erpipomoea* Choisy, Mém. Soc. Phys. Genève 6: 444. 1833. TYPE: *I. pes-caprae* (L.) R. Br.
I. sect. *Pes-caprae* Griseb., Fl. Brit. W. Ind. 470. 1864.

a. Flowers white, with light or dark throat inside tube.
  b. Leaves sagittate ..... 9. *I. aquatica*
  bb. Leaves mostly oblong to ovate-oblong, blades rounded at base ..... 12. *I. stolonifera*
aa. Flowers pink, lavender or purple.
  c. Leaves rounded-cordate, apically acute ..... 10. *I. asarifolia*
  cc. Leaves suborbicular, apically emarginate ..... 11. *I. pes-caprae*

9. **Ipomoea aquatica** Forsk., Fl. Aegypt. Arab. 44. 1775. TYPE: Yemen, Zepid, *Forskal* (not seen).

Convolvulus reptans auct. non L. (1753).

Vines; stems hollow, rooting at the nodes, procumbent on wet ground or floating on water, glabrate. *Leaves* mostly hastate, the terminal lobe narrowly triangular or lanceolate, the basal lobes smaller and spreading or almost absent, 4–12 cm long, apically acute or obtuse, glabrescent. *Flowers* solitary or in few-flowered cymes, the inflorescence glabrous; sepals ovate-oblong, subequal, 7 mm long, obtuse or subacute, mucronulate, glabrous; corolla white or purple, 4–5 cm long, funnelform. *Fruits* capsular, ovoid to globose, 8–10 mm long; seeds densely soft-pilose or glabrous.

Ipomoea aquatica flowers in January, March and July. A native of the Old

World tropics, it now occurs in the West Indies, Guatemala, British Honduras, Costa Rica, Panama and northern South America.

This Old World species is fairly widely distributed in the New World because of its use as a vegetable. It is distinguished from the other species in this group by the flowers with purple throats and lighter lavender or white limbs. There are some races with completely white flowers.

BOCAS DEL TORO: Changuinola Valley, *Dunlap 404* (F, US). CANAL ZONE: Río Agua Salud near Frijoles, *Piper 5836* (US). Near Juan Mina, *Bartlett & Lasser 16537* (MO).

10. **Ipomoea asarifolia** (Desr.) Roem. & Schult., Syst. Veg. 4: 251. 1819.

Convolvulus asarifolius Desr. *in* Lam. Encycl. Méth. 3: 562. 1789. TYPE: Senegal, *Roussillon* (not seen).

Vines; stems herbaceous, decumbent and twining, rooting at the nodes glabrous. *Leaves* rounded-cordate to subreniform, 4–8 cm long, basally cordate, apically rounded, glabrescent. *Flowers* solitary or in axillary or terminal simple or compound cymes, glabrous to puberulent; sepals unequal, the outer sepals 5–6 mm long, the inner sepals 10–12 mm long, elliptic to ovate, coriaceous, rounded apically, mucronate, glabrous; corolla lavender to purple, 6–8 cm long, funnelform. *Fruits* tardily dehiscent capsules, subglobose, 10–12 mm long, brown, glabrous; seeds brown to dark brown 6–7 mm long, minutely gray-pubescent.

This species flowers in July and from September through February. It occurs in Mexico (Chiapas), Guatemala, Honduras, Panama, West Indies, South America, and tropical Asia and Africa. "Batatilla de cienaga"; "campanilla."

Ipomoea asarifolia is much like *I. pes-caprae* in aspect. The two may be separated by leaf shape: cordate-orbicular to subreniform and apically acute to obtuse in *I. asarifolia*, mostly ovate to obovate and always apically emarginate in *I. pes-caprae*.

CANAL ZONE: Panamá, collector unknown, *1935* (MO). COCLÉ: Between Aguadulce and Antón, *Woodson et al. 1215* (MO). Aguadulce, *Pittier 4911* (US). Between Porto Posada and Penonomé, *Williams 156* (US). DARIÉN: Without locality, *Macbride 2674* (US). HERRERA: Road from Chitré to Divisa, *Burch et al. 1354* (MO). PANAMÁ: 1 mi. W of Bejuco, *Tyson & Blum 2539* (MO). Between hunting club and El Congor Hill on Río Jagua, *Hunter & Allen 469* (MO, US). Laguna de Portala near Chepo, *Pittier 4618* (US). Between Las Sabanas and Matías Hernández, *Standley 31803* (US). Las Sabanas, *Standley 25828, 25829* (both US). Nuevo San Francisco, *Standley 30698, 30707, 30746* (all US). Near Punta Paitilla, *Standley 26301* (US); *Piper 5405* (US). Between Savanas and Río Yguana, *Macbride 2674* (F). Penonomé, *Dwyer 7055* (MO). Near Santiago, *Allen 1083* (F, MO).

11. **Ipomoea pes-caprae** (L.) R. Br. *in* Tuckey, Narr. Exped. R. Zaire. 477. (March 1818); Sweet (July 1818, redundant combination).

Convolvulus pes-caprae L., Sp. Pl. 159. 1753. TYPE: India, Linn. herb: (LINN 218-59 not seen; microfiche).

C. brasiliensis L., Sp. Pl. 159. 1753. TYPE: Based on *Convolvulus marinus catharticus. . . .* Plumier, Descr. Pl. Amer. *t. 104.* 1693.

C. bilobatus Roxb., Fl. Ind. ed. Carey & Wall. 2: 73. 1824. TYPE: India, *Wallich* (K, not seen; microfiche).

Ipomoea pes-caprae (L.) Sweet var. *emarginata* Hall. f., Bull. Soc. Roy. Belgique 37: 98. 1898. TYPE: Based on *Convolvulus brasiliensis* L.

I. pes-caprae (L.) Sweet subsp. *brasiliensis* (L.) Ooststr., Blumea 3: 533. 1940. TYPE: Brazil, *Plumier* (not seen).

Vines; stems long-trailing and rooting at the nodes, perennial with a thickened taproot, glabrous. *Leaves* often secund, ovate, obovate, elliptic, orbicular, or transverse-elliptic to reniform, 3–10 cm long, basally truncate, attenuate or cordate, apically mostly emarginate, rarely truncate, mucronulate, fleshy, glabrous. *Flowers* in mostly 1-flowered, occasionally cymose inflorescences, glabrous; sepals subequal, the outer sepals ovate to broadly elliptic, the inner sepals mostly orbicular, 5–11 mm long, obtuse and mucronulate, glabrous, subcoriaceous; corolla limb pink to lavender-purple, throat darker purplish within, 3–5 cm long. *Fruits* capsular, ovoid to depressed-globular, 12–17 mm in diameter, glabrous; seeds black, densely brownish-tomentose.

This pantropical species flowers all year.

The only purple-flowered emarginate-leaved morning glory growing on the beaches of Panama, this is easily recognized.

BOCAS DEL TORO: Sta. Catalina, *Blackwell et al. 2690* (MO). CANAL ZONE: Chagres, *Fendler 239* (MO, US). COLÓN: María Chiquita, *Ebinger 438* (MO). Fató, *Pittier 5725* (US). LOS SANTOS: Monagre Beach, *Lewis et al. 1670* (MO). PANAMÁ: Old Panama City, *Greenman & Greenman 5148* (F). San José Island, *Harlow 90* (US). Peña Prieta, *Bro. Heriberto 238* (US). San José Island, *Johnston 851* (MO). Punta Paitilla, *Standley 30802* (US). VERAGUAS: Mouth of Río Concepción, *Lewis et al. 2852* (MO).

12. **Ipomoea stolonifera** (Cyrill.) Gmelin, Syst. Nat., ed. 13. 2: 345. 1791.

Convolvulus littoralis L., Syst. Nat., ed. 10. 924. 1759. TYPE: Based on *Convolvulus foliis obtusis*. . . . Plumier, Pl. Amer. 79, *t. 90, f. 2*. 1756.
C. stoloniferus Cyrill., Pl. Rar. Neap. 1: 14, *t. 5*. 1788.
Ipomoea littoralis Boiss., Fl. Orient. 4: 112. 1879, non Blume (1826).

Vines; stems trailing and rooting at the nodes, perennial, glabrous. *Leaves* variable in shape, often linear, lanceolate, ovate to oblong and the margins entire or undulate all on the same plant, 1.5–4(–8) cm long, the size varying greatly with habitat, basally obtuse, truncate to cordate, apically obtuse, emarginate or occasionally 2-lobed, glabrous. *Flowers* usually solitary in leaf axils; sepals oblong, the inner sepals 10–15 mm long, the outer sepals shorter, acute to obtuse, mucronulate, glabrous, subcoriaceous; corollas with the limb white, the throat apically yellow and basally purple, 3.5–5 cm long. *Fruits* capsular, globular, rarely ovoid, 10 mm in diameter; seeds light brown, short-tomentose and with longer comose trichomes on the margins.

This species flowers from December to April. It is pantropical, but it occurs mostly in Atlantic coastal areas.

The white flower with the yellow throat apex and purple throat base is distinctive.

BOCAS DEL TORO: Changuinola Valley, *Dunlap 537* (F, US). Bocas del Toro, *Carleton 159* (US). CANAL ZONE: Galeta Island, *D'Arcy s.n.* (MO). Chagres, *Fendler 240* (F, MO, US). Shady beach area, Coco Solo, *Gentry 4851* (MO). VERAGUAS: Mouth of Río Concepción, *Lewis et al. 2763* (MO).

Group 4. ERIOSPERMUM

Ipomoea sect. *Eriospermum* Hall. f., Bot. Jahrb. (Syst.) 18: 149. 1893. TYPE: *I. digitata* L.
I. subg. *Eriospermum* (Hall. f.) Verdcourt, Taxon 6: 152. 1957.

a. Erect to scrambling shrubs ..... 15. *I. carnea*
aa. Twining lianas or vines.
  b. Stamens exserted for about half their length; corollas red to red-purple, the limb strongly reflexed ..... 18. *I. mirandina*
  bb. Stamens included within the corolla tube; corollas red, pink, purple or white, the limb rotate to campanulate.
    c. Sepals and stems covered with long spreading setae or fleshy tentacular projections, those on stems often drying black ..... 20. *I. setosa*
    cc. Sepals and stems merely glabrous or pubescent, never with fleshy outgrowths.
      d. Leaves deeply palmate-lobed almost to the base or costa ..... 17. *I. mauritiana*
      dd. Leaves entire or rarely slightly lobed.
        e. Leaves densely and conspicuously white- to yellowish-pubescent beneath. ..... 21. *I. tuxtlensis*
        ee. Leaves glabrous or inconspicuously pubescent beneath.
          f. Sepals subequal in length.
            g. Flowers funnelform, lavender or purple, 5–8 cm long ..... 19. *I. phillomega*
            gg. Flowers campanulate, pink or white, 4–5 cm long ..... 14. *I. batatoides*
          ff. Sepals unequal, the outer shorter than inner.
            h. Corollas white with a purple to lavender throat, 6–7 cm long ..... 13. *I. anisomeres*
            hh. Corollas yellowish or greenish with purple markings usually on the limb, 5–6 cm long ..... 16. *I. lindenii*

13. **Ipomoea anisomeres** Rob. & Bartl., Proc. Amer. Acad. Arts 43: 57. 1907. TYPE: Guatemala, Zacapa, *Deam 318* (GH, lectotype, not seen).

Vines; stems mostly slender, herbaceous, smooth but becoming papillate with age, glabrous. *Leaves* oblong-ovate, broadly ovate to sagittate, 3–7 cm long and 2–7 cm wide, basally cordate to sagittate, apically acute to acuminate, glabrous or at least glabrescent. *Inflorescences* cymose to subcorymbose, 1- to several-flowered, glabrous. *Flowers* white with a purple to lavender throat; sepals unequal, the outermost orbicular to oval, the inner oblong to ovate, 1–10 mm long, glabrous; corollas narrowly funnelform, 6–7 cm long. *Fruits* ovoid, shortly apiculate, to 10 mm in diameter; seeds comose with light colored trichomes.

This species flowers in February. It occurs in Mexico (Vera Cruz), Guatemala and Panama.

The collection *Tyson & Lazor 6163* could be referred to var. *sagittiformis* L. O. Wms. (Fieldiana: Bot. 32: 185. 1970) based on leaf shape. This species, however, belongs to an alliance where leaf shape is unusually variable; I prefer to recognize no infraspecific taxa until the populations are better known.

CANAL ZONE: Gaillard Highway between Paraíso and Summit, *Croat 13256* (MO). 2 mi. N of Cocoli near Contractors Hill, *Tyson & Lazor 6163* (MO).

14. **Ipomoea batatoides** Choisy, Mém. Soc. Phys. Genève 8: 136. 1838, non Benth. (1840). TYPE: Brazil, Bahia, *Blanchet* (not seen).

I. microsticta Hall. f., Bull. Herb. Boissier, Sér. 1. 7: 411. 1899. TYPE: Guatemala, Escuintla, *Seler 2427* (not seen).

I. glabriuscula House, Bot. Gaz. (Crawfordsville) 43: 409. 1907. TYPE: Guatemala, *Heyde 1892* (US, not seen).

Lianas; stems herbaceous at the tips, becoming woody with age, glabrous. *Leaves* broadly ovate to suborbicular, 3–10 cm long, shallowly cordate to truncate basally, acuminate apically, glabrous or obscurely puberulent and with microscopic "glands" beneath. *Flowers* disposed in a 1- to several-flowered axillary cyme; sepals elliptic to suborbicular, 6–8 mm long, subcoriaceous and cochleate; corollas pale pink to white, 4–5 cm long. *Fruits* capsular, broadly ovoid, apically attenuate to the base of the persistent style; seeds comose.

This species flowers from November to March. It occurs in Mexico, Guatemala, British Honduras, Costa Rica, Panama and South America.

BOCAS DEL TORO: Hillside above Almirante, *Gentry 2679* (MO). CANAL ZONE: Past the Pacific Saddle Club, *Blum 2057* (MO). Pipeline Road, 12 mi. from Gamboa gate, *Croat 12745* (MO). Madden Forest Road at entrance to Boy Scout Road, *Croat 12897, 12898* (MO). Near Summit, *Dodge & Allen s.n.* (MO-1120260). Las Cascadas Plantation, *Standley 25823, 29576* (both US). Between Fort Clayton and Corozal, *Standley 29057* (US). Madden Dam, collector unknown, 1935 (MO). CHIRIQUÍ: Between Hato del Jobo and Cerro Vaca, *Pittier 5405* (F, MO). COCLÉ: Road to El Cope, *Burch et al. 1367* (MO). El Valle de Antón, *Lewis et al. 2579* (MO). COLÓN: Penonomé, Along Santa Rita Ridge road, ca. 20 mi. E of Colón, *Gentry 464* (MO); *Williams 391* (NY, US). PANAMÁ: Hills above Campana, *Allen 1322* (F, MO). Santa Rita Ridge, *Croat 13850* (MO). Hills between Campana and Potrero, *Dodge & Allen 8641* (MO). SE slope of Cerro Campana, *Lewis et al. 3129* (MO).

15. **Ipomoea carnea** Jacq., Enum. Pl. Carib. 13. 1760. TYPE: Colombia, Cartagena *Jacquin* (not seen).

I. fistulosa Mart. *ex* Choisy *in* DC., Prodr. 9: 349. 1845. LECTOTYPE: Brazil, *Martius 2398* (M).

Batatas? *crassicaulis* Benth., Voy. Sulphur 5: 134. 1845. TYPE: Ecuador, Guayaquil, *Sinclair* (K, not seen).

Ipomoea crassicaulis (Benth.) Rob., Proc. Amer. Acad. Arts 51: 530. 1916.

Shrubs to 2.5 m high; stems woody at the base, herbaceous at the tips, hollow, glabrous or minutely puberulent. *Leaves* suborbicular, ovate to lanceolate, 10–25 cm long, truncate to shallowly cordate basally, long acuminate apically, puberulent on both surfaces but sometimes glabrescent. *Flowers* in cymose-paniculate clusters at the branch tips, 1- to several-flowered; sepals suborbicular, 5–6 mm long, subcoriaceous, glabrate or puberulent; corollas deep pink to rose-purple, the throat darker than the limb, 5–8 cm long, finely tomentose outside. *Fruits* capsular, ovoid to subglobose, 2 cm long, 1–1.5 cm in diameter; seeds covered with long comose brown trichomes.

This pantropical species of New World origin flowers all year.

Apparently Verdcourt (1963) has been the only person to recognize the similarity between *I. carnea* and *I. fistulosa*. Details of why they should be considered synonymous will be published elsewhere. This is the only shrub *Ipomoea* in Panama.

CANAL ZONE: Along Las Cruces Trail, *Hunter & Allen 723* (MO). Fort Clayton, *Lewis et al. 296* (MO); *Tyson 3462* (MO). COCLÉ: Between Aguadulce and Antón, *Woodson et al. 1211* (MO). DARIÉN: Near Yaviza, *Stern et al. 105* (US). HERRARA: Chitré to Davisa, *Burch et al. 1359* (MO). LOS SANTOS: Playa de La Concepción, *Burch et al. 1226* (MO). PANAMÁ:

Near La Jagua, *Bartlett & Lasser 17002* (MO). Las Sabanas, *Bro. Heriberto 20* (US). Between El Jagua Hunting Club and El Congor Hill, *Hunter & Allen 468* (MO). Sabanas, *Bro Paul 417* (US). Near Bella Vista, *Piper 5378* (US). Las Sabanas, *Standley 30691* (US). Tapia, *Stevens 1012* (US). VERAGUAS: Puerto Mutis, *Tyson 5186* (MO).

16. **Ipomoea lindenii** Mart. & Gal., Bull. Acad. Bruxelles 12, 2: 264. 1845. SYNTYPES: Zacuapan, Mexico, *Galeotti 1360*; *Linden 301* (neither seen).

I. niocyana House, Ann. New York Acad. Sci. 18: 231. 1908. TYPE: Costa Rica, forest near Nicoya, *Tonduz 13671* (NY, holotype).

Vines; stems often becoming suffrutescent, glabrous. *Leaves* cordate-ovate to subsagittate, 5–10 cm long, acuminate apically, rounded to acuminate on the basal lobes, mucronate, glabrous to sparsely pubescent along the veins. *Flowers* in 1–2-flowered cymes; sepals unequal, oblong or lanceolate-oblong, 6–8 mm long, obtuse apically, glabrous to slightly pubescent; corollas yellowish to greenish, 5–6 cm long. *Fruits* ovoid, apiculate, to 10 mm in diameter; seeds comose with whitish trichomes.

This species flowers from December to January. It occurs in Mexico and Panama.

This *Ipomoea* belongs to a complex of species from Mexico and Central America which needs study. There is a series of morphs, most of which have names.

CANAL ZONE: Cerro Galera, *Gentry 6614* (MO). LOS SANTOS: 25 mi. SW of Tonosí, *Lewis et al. 2905* (MO). PANAMÁ: Between Capira and Potrero, *Dodge & Hunter 8633* (MO). SE slope of Cerro Campana, *Lewis et al. 3124* (MO). Río Tapia, *Standley 26206, 28102, 28294* (all US).

17. **Ipomoea mauritiana** Jacq., Coll. 4: 216. 1791. TYPE: A plant from Mauritius cultivated at Vienna, probably not preserved.

Convolvulus paniculatus L., Sp. Pl. 156. 1753. LECTOTYPE: India; illustration of *Flos passionis spurius malabaricus* . . . . Rheede, Hort. Malabar. 11. *t. 49*. 1697.
Ipomoea digitata auct. non L. (1759).
I. paniculata (L.) R. Br., Prodr. 486. 1810, non Burm. (1768).

Vines; stems woody below, herbaceous nearer the tips, glabrous. *Leaves* orbicular in outline, palmately lobed with (3–)5–7(–9) lobes, rarely entire, 5–8 cm long, cordate or truncate basally, the lobes ovate, acuminate apically, glabrous or with scattered trichomes. *Flowers* in few- to many-flowered cymose inflorescences; sepals orbicular or elliptic, 6–12 mm long, markedly convex and clasping the corolla, subcoriaceous, glabrous; corollas reddish-purple to rose pink, 4–6 cm long. *Fruits* capsular, ovoid, 1.2–1.4 cm long, glabrous; seeds black, comose.

This species flowers from August to June, probably all year. It is pantropical in distribution.

For many years this species has been confused with *I. digitata* of Linnaeus. Linnaeus' species is endemic to the island of Hispaniola and differs in several aspects from *I. mauritiana*. *Ipomoea mauritiana* is pantropical, commonly col-

lected near sea shores; its palmately lobed leaves and purplish flowers are distinctive.

BOCAS DEL TORO: Near Chiriquí Lagoon, *Wedel 1310* (MO), *1177* (MO, US), *2678*, *2734* (both MO). CANAL ZONE: Ancón, *Mason 5* (F, US). CHIRIQUÍ: Between Pinola and Quebrada Seco, *Kirkbride & Duke 1022* (MO). COLÓN: María Chiquita, *Dwyer s.n.* (MO). DARIÉN: Río Chico, *Allen 4647* (MO). PANAMÁ: Isla de Pedro Gonzales, *Dwyer 1724*, *1758* (both MO). Taboga Island, *Pittier 3609* (US). SAN BLAS: Beach E of Puerto Obaldía, *Croat 16902* (MO). Mulatuppu, *Duke 8535* (MO). Near Mandinga, *Duke 8881* (MO). Island Soskatupu, *Kirkbride 197A* (MO). Puerto Obaldía, *Pittier 4392* (US).

18. **Ipomoea mirandina** (Pittier) O'Donell, Lilloa 26: 370. 1953.

Exogonium mirandinum Pittier, Jour. Washington Acad. Sci. 21: 143. 1931 TYPE: Venezuela, Miranda, *Pittier 12217* (US, isotype).

Lianas; stems herbaceous toward the tips, woody toward the base, glabrous. *Leaves* ovate to cordate-ovate, 7–20 cm long, subtruncate to cordate basally, acuminate apically, glabrate. *Flowers* in axillary cymes; sepals broadly oblong to suborbicular, 1.5–2 cm long, subequal, glabrous; corollas lavender to magenta, salverform, 5.5–7 cm long, the tube more or less cylindric, the limb flaring, usually reflexed. *Fruits* not seen.

Ipomoea mirandina flowers in December. Previously known from only Venezuela this species may be confused with *I. phillomega* to which it may be very closely related. The flowers in *I. mirandina* are adapted for bird pollination and the anthers are exserted from the corolla tube; the limb is reflexed.

CANAL ZONE: Near Salamanca, *Dodge et al. 16978* (MO). DARIÉN: Camp Summit, *Oliver et al. 3660* (MO). PANAMÁ: Cerro Campana, below FSU cabin, *Gentry 5768* (MO). SW slope of Cerro Campana, *Lewis et al. 3155* (MO).

19. **Ipomoea phillomega** (Vell.) House, Ann. New York Acad. Sci. 18: 246. 1908.

Convolvulus phillomega Vell., Fl. Flum. 74. 1825; Icones 2: *pl. 63*. 1827. TYPE: Argentina (not seen).

Ipomoea demerariana Choisy *in* DC., Prodr. 9: 361. 1845. TYPE: Guyana, Demerara, *Parker* (K, not seen).

I. cardiosepala Meisn. *in* Mart., Fl. Bras. 7: 265. 1869. TYPE: Rio de Janeiro, Brazil, *Burchell 1865* (not seen).

I. magnifolia Rusby, Mem. Torrey Bot. Club 6: 84. 1896. TYPE: Bolivia, *Bang 1277* (NY, not seen).

Lianas; stems woody below, herbaceous above, glabrate. *Leaves* rounded-cordate, 8–20 cm broad, about as long as broad, acute or cuspidate-acuminate, cordate basally, glabrate or pilose beneath along the veins. *Flowers* usually clustered; sepals broadly ovate, 15–18 mm long, obtuse to subacute, often drying purplish, pilose to glabrescent; corollas purple, the throat darker, 5–8 cm long. *Fruits* capsular, subglobose, glabrous, 1 cm in diameter; seeds comose.

This species flowers from June to February, probably all year. It occurs in British Honduras, Guatemala to Guyana, Peru and the Lesser Antilles.

Most authors separate *I. phillomega* from *I. demerariana*, but I find no grounds for this. After examining living plants in Peru and studying specimens in several

herbaria, I am convinced that these names apply to a widespread, somewhat variable species. The large cordate leaves are characteristic. It commonly grows along waterways.

BOCAS DEL TORO: Isla Colón, *Wedel 514* (MO). Water Valley, *Wedel 729* (MO). Old Bank Island, *Wedel 2116* (MO, US). Isla Colón, *Wedel 2805* (MO, US). Big Bight, *Wedel 2881* (MO, US). CANAL ZONE: Barro Colorado Island, *Aviles 4, 5* (both F); *Bailey 632* (F); *Bangham 546* (F, US). Road S-10 near junction with road S-1, N of Escobal, *Croat 12475* (MO). Near Summit, *Dodge & Hunter 8650* (MO); *Fairchild 10* (F); *Kenoyer 503A* (US); *Shattuck 1110* (F); *Starry 245* (F). Agua Clara, *Pittier 3981* (US). Barro Colorado Island, *Standley 41018* (US); *Wetmore & Woodson 90* (F). COLÓN: Near Sardinilla, *Blum & Tyson 475* (MO). Along Río Iguanitos, *Elias & Kirkbride 1633* (MO). Road to Piña, *Kirkbride & Hayden 315* (MO). Fató, *Pittier 3835* (F, US). Gatun Lake, *Seibert 1523* (MO, US). DARIÉN: Near mouth Río Yapé, *Allen 325* (MO). Near Boca de Cupe, *Allen 907* (MO). Cocalito, *Dwyer 4461A* (MO). Near El Real, *Stern et al. 747* (MO, US). Near Río Sabana and Lara, *Tyson et al. 4720* (MO). PANAMÁ: Isla Pedro Gonzales, *Dwyer 1723* (MO). 5 mi. SW of Cerro Brewster, *Lewis et al. 3423* (MO). Near Arenoso, *Seibert 607* (MO). Near Chorrera, *Woodson et al. 1676* (MO). VERAGUAS: Caribbean slope above Río Primero Brazo, 5 mi. NW of Santa Fé, *Liesner 1020* (MO).

20. **Ipomoea setosa** Ker., Bot. Reg. 4: 5. 335. 1818. TYPE: (not seen).

I. melanotricha Brandeg., Univ. California Publ. Bot. 4: 381. 1913. TYPE: Mexico: Zacuapan, *Purpus 5747* (not seen).

Vines; stems herbaceous and covered with scattered fleshy trichome-like structures, these often drying black. *Leaves* suborbicular to ovate in outline, deeply 3–7-lobed, 10–20 cm long, cordate basally, the lobes ovate to lanceolate, acuminate. *Flowers* solitary or in 3–12-flowered cymose clusters, covered with fleshy trichomes; sepals oblong, 10–14 mm long, obtuse, subcoriaceous, covered with fleshy trichomes; corollas pink to lavender, salverform, the tube 5–6 cm long, the limb campanulate to subrotate. *Fruits* capsular, subglobose to depressed-globose, 1.5–2 cm in diameter; seeds comose.

Ipomoea setosa flowers in January. It ranges from Mexico to South America.

This is the only species outside the *Calonyction* group with light colored salverform corollas; the flowers open after midnight and close shortly after dawn. Since it is self-compatible, the seed set is high. The species is widely spread around the world.

LOS SANTOS: 10 mi. N Tonosí, *Tyson et al. 2950* (MO).

21. **Ipomoea tuxtlensis** House, Ann. New York Acad. Sci. 18: 256. 1908. TYPE: Chiapas, Mexico, *Nelson 3094* (US, holotype).

Vines; stems herbaceous, perennial, mostly densely white pubescent. *Leaves* ovate to cordate, 5–15 cm long, cordate to truncate basally, entire or occasionally 3-lobed, the lobes acute or obtuse, appressed-pilose above, densely white to yellowish sericeous beneath. *Flowers* few to many, peduncles usually less than 2 cm long; sepals oblong-ovate, 10–12 mm long, the outer sericeous, rounded apically, the inner glabrous or slightly pubescent, retuse; corollas dark purple to purple-red, 3.5–6 cm long. *Fruits* capsular, globose, glabrous, 1 cm in diameter; seeds densely comose.

This species flowers from July to March, probably all year. It occurs in southern Mexico, Guatemala, British Honduras and Panama.

This is the only species of *Ipomoea* in Panama with leaves densely sericeous beneath.

PANAMÁ: Cerro Jefe, *Correa et al. 1587* (MO); *Dressler 3040* (MO). Toward top of Cerro Campana, *Duke 5968* (MO). Cerro Jefe, *Duke 9445* (MO). Ca. 8 mi. S of Goofy Lake, *Dwyer 7087* (MO). Cerro Jefe, *Dwyer & Guager 7333* (MO); *Gentry 2118, 6135* (both MO). Cerro Campana, *Gentry 5759* (MO). Near Cerro Jefe, *Lewis & Dressler 7554* (MO). Cerro Azul, *Porter et al. 4075* (MO); *Tyson 2114* (MO). Cerro Jefe, *Tyson et al. 4292* (MO).

Group 5. ORTHIPOMOEA

Ipomoea sect. *Orthipomoea* Choisy *in* DC., Prodr. 9: 353. 1845. TYPE: *I. heterophylla* R. Br. 1819.

a. Leaves lobed almost to the base or to the costa.
  b. Leaves sessile, divided to the base into filiform lobes; plants usually erect and not twining ..... 22. *I. capillacea*
  bb. Leaves petiolate, the lobes linear or broader; plants usually twining ..... *I. wrightii*
aa. Leaves entire or only slightly lobed.
  c. Corollas 10–25 mm long.
    d. Flowers yellow, 10–15 mm long ..... 24. *I. minutiflora*
    dd. Flowers blue or purple, 20–25 mm long ..... *I. aristolochiaefolia*
  cc. Corollas 30 mm long or longer.
    e. Leaves densely pubescent beneath ..... 25. *I. squamosa*
    ee. Leaves glabrous or inconspicuously pubescent beneath.
      f. Corollas pubescent outside, 3 cm long ..... *I. parasitica*
      ff. Corollas glabrous outside, 4–8 cm long.
        g. Corollas blue with a white to yellowish throat ..... *I. tricolor*
        gg. Corollas white to purple.
          h. Corollas purple ..... 25. *I. squamosa*
          hh. Corollas white ..... 23. *I. chiriquiensis*

22. **Ipomoea capillacea** (H.B.K.) G. Don, Gen. Syst. 4: 267. 1838.

Convolvulus capillaceous H.B.K., Nov. Gen. Sp. Pl. 3: 97. 1819. TYPE: Colombia, *Bonpland* (not seen).

Ipomoea muricata Cav., Icon. 5: 52, *t. 478, fig. 2.* 1799, non Jacq. (1798). TYPE: *Cavanilles* (not seen).

I. armata Roem. & Schult., Syst. Veg. 4: 214. 1819. Nom. nov. for *Ipomoea muricata* Cav.

I. muricatisepala Matuda, Ann. Inst. Biol. Méx. 34: 124. 1964. Nom. nov. for *Ipomoea muricata* Cav.

Herb; stems erect, simple or branching from a perennial ovoid to rotund tuberous root, often twining at the tips and reaching 40 cm in length, glabrous or glabrescent. *Leaves* sessile, dissected into filiform segments, 1–2 cm long, glabrous. *Flowers* solitary on short peduncles in the leaf axils; sepals oval to broadly ovate, 4–5 mm long, obtuse, aristate, sparsely to densely muricate outside; corolla bright pink to purple on the upper tube and limb, the lower tube white, 2–2.5 cm long. *Fruits* capsular, subglobose to globose, 4–5 mm in diameter, brown, glabrous, the 4 seeds usually 2.5 mm long, 1.5–2 mm broad, finely pubescent with short reddish-brown trichomes.

This species flowers in June, July and August. It ranges from the southwestern United States to northwestern South America.

FIGURE 9. *Ipomoea chiriquensis* Standl., habit (× ⅗). [After *Allen 1512* (MO).]

This is one of the easiest species of *Ipomoea* to recognize in Panama because of the erect, herbaceous habit, filiform leaf divisions, and tuberous root. All Panamanian collections have been collected from upland savanna or llanos areas.

CHIRIQUÍ: Llano del Volcán, *Allen 4847* (F). Boquete, *Davidson 1063* (F, MO, US). El Hato de Volcán, *Ebinger 773* (US). Llanos del Volcán, *Seibert 341* (MO). Near Boquete, *Stern et al. 1163* (MO).

23. **Ipomoea chiriquiensis** Standl., Ann. Missouri Bot. Gard. 27: 334. 1940. TYPE: Panama, *Allen 1512* (MO, holotype; F, isotype).—FIG. 9.

Vines; stems herbaceous, glabrous. *Leaves* ovate-cordate, 10–19 cm long, membranaceous, basally cordate, apically acuminate. *Flowers* in cymes of 2–6 flowers per cyme; sepals unequal, the exterior sepals oblong-lanceolate, 6–7 mm long, acuminate, the interior sepals oval to broadly ovate, 12–14 mm long, shortly mucronate; corollas white, 5 cm long, the limb 8 cm wide. *Fruits* unknown.

Known only from 2 collections, this species is similar in many facies to *I. squamosa*. It flowers in January and February.

CHIRIQUÍ: Trail from Paso Ancho to Monte Lirio, upper valley of Río Chiriquí Viejo, 1500–2000 m, *Allen 1512* (MO, F). Near Methodist Camp near Nueva Swissa, *Croat 13504* (MO).

24. **Ipomoea minutiflora** (Mart. & Gal.) House, Muhlenbergia 5: 71. 1909.—FIG. 10.

Convolvulus minutiflorus Mart. & Gal., Bull. Acad. Bruxelles 12(2): 262. 1845. TYPE: Mexico, Oaxaca, *Galeotti 1372* (photo).
Ipomoea filipes Benth. *ex* Meisn. *in* Mart., Fl. Bras. 7: 274. 1869. TYPE: Brazil, Pará, *Spruce* (not seen).

Vines; stems slender and herbaceous, annuals, pilose, glabrescent. *Leaves* broadly ovate to subreniform, 1–3(–7) cm long, acute to rounded apically, cordate basally, entire to somewhat angulate, glabrous beneath, ciliate, pilose above. *Flowers* on peduncles usually longer than the leaves, 1–3-flowered; sepals sublanceolate, 2–2.5 mm long, acute to acuminate, white pilose; corollas yellow to pale yellow, 10–15 mm long. *Fruits* capsular, subglobose, 3–4 mm in diameter; seeds black, minutely puberulent but glabrate.

Ipomoea minutiflora flowers from December to February. It is distributed through southern Mexico, Central America and northern South America.

This species is similar to *I. aristolochiaefolia* but is separated from that species by the small yellow flowers.

CANAL ZONE: Boy Scout Road, *Croat 12913* (MO). Madden Dam, *Dwyer 3038* (MO). Las Cruces Trail, *Hunter & Allen 692* (MO). PANAMÁ: Vera Cruz, *Lewis et al. 3004* (MO). Río Tocumen, *Standley 29431* (US).

25. **Ipomoea squamosa** Choisy *in* DC., Prodr. 9: 376. 1845. TYPE: Brazil, *Martius* (P, not seen).

I. morelli Duchass. & Walp., Linnaea 23: 752. 1850. TYPE: Panama, *Duchassaing* (not seen).
I. callida House, Muhlenbergia 3: 42. 1907. TYPE: Honduras, *Wilson 534* (NY, not seen).

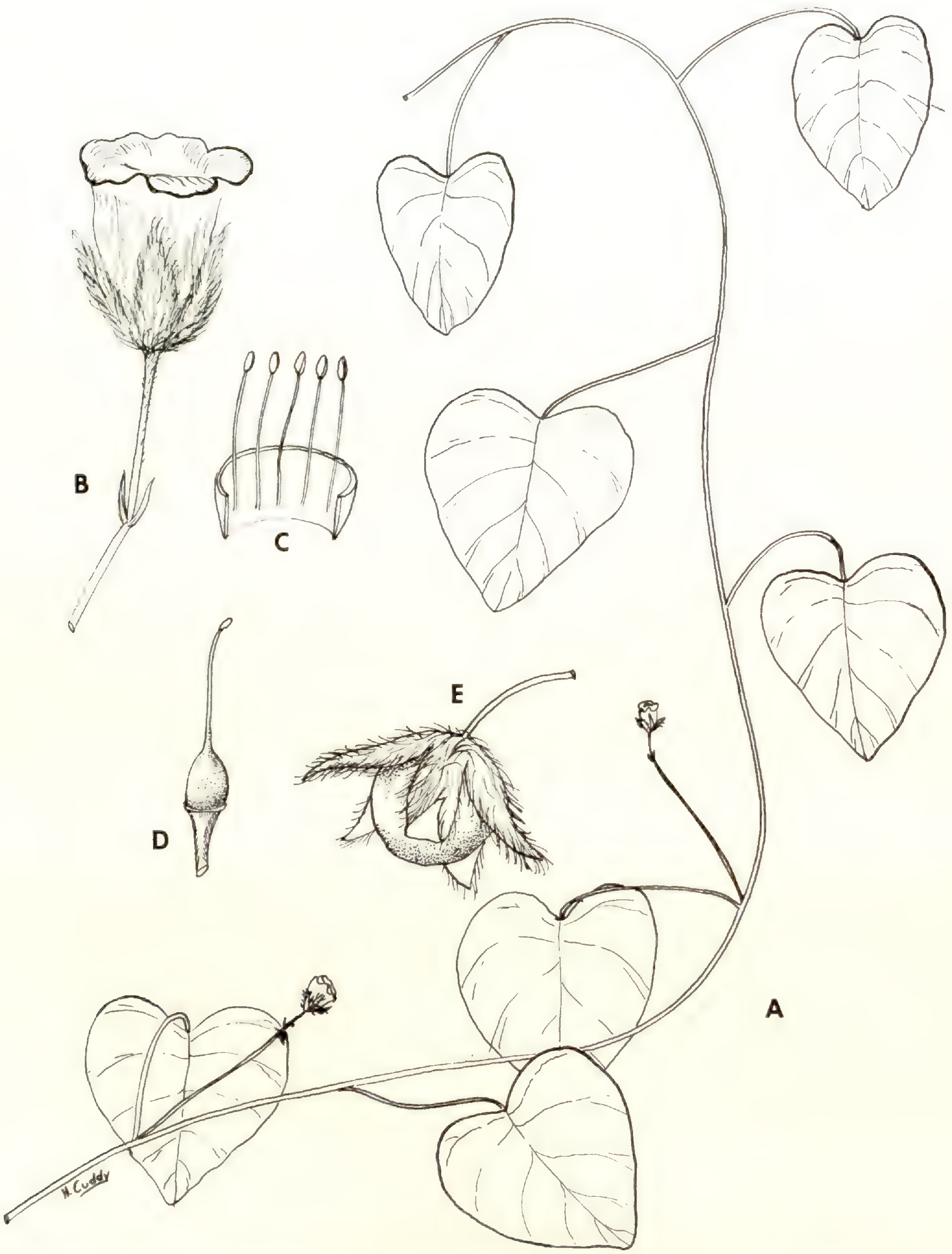

FIGURE 10. *Ipomoea minutiflora* (Mart. & Gal.) House.—A. Habit (× 1⅕).—B. Flower (× 6).—C. Dissection of corolla with stamen attachment (× 6).—D. Gynoecium (× 6).—E. Fruit (× 6).

I. wilsonii House, Muhlenbergia 3: 44. 1907. TYPE: Honduras, *Wilson 530* (NY, not seen).
I. vestallii Standl., Contr. Arnold Arbor. 5: 130. 1933. TYPE: Panama, Barro Colorado Island, *Shattuck 785* (F-652503, holotype).

Vines; stems herbaceous to suffrutescent, glabrous. *Leaves* variable in shape but usually subsagittate in outline, cordate, sagittate to hastate, long-acuminate apically, variable basally, glabrous to pubescent on both surfaces. *Flowers* on peduncles usually equaling or longer than the petioles, in simple cymose to 10-flowered cymes; sepals ovate to suborbicular, the outer 3–5 mm long, the inner 5–10 mm long, rounded to truncate apically, glabrous, the margins scarious; corolla bluish, pink to purplish, (4–)5–8 cm long. *Fruits* not seen.

This species flowers from December to March. It ranges from Mexico and Central America into South America.

While I have placed this species in *Orthipomoea*, I am not certain it belongs here. It is similar to the *I. lindenii* complex of *Eriospermum* and may belong there; however, Standley (Contr. U. S. Natl. Herb. 27: 312–317. 1928) stated that the seeds are finely pubescent. The pubescence type suggests affinity here and not with *Eriospermum*.[6]

CANAL ZONE: Barro Colorado Island, *Croat 7777, 14006* (both MO). Valley of Río Puente, *Dodge & Allen 17313* (MO). Chagres, *Fendler 242* (MO). 1–3 mi. from Gorgona, *Maxon 4729* (F, US). Gatún, *Pittier 2561* (US). Around Gamboa, *Pittier 2601* (US). Between Río Grande and Pedro Vidal, *Pittier 2704* (US). Barro Colorado Island, *Shattuck 785* (F). Gamboa, *Standley 28310* (US). Between Fort Clayton and Corozal, *Standley 29123* (US). Barro Colorado Island, *Wetmore & Abbe 192* (F). Near Drayton House, *Woodworth & Vestal 563* (F). Barro Colorado Island, *Woodworth & Vestal 579* (F). COLÓN: Juan Mina above Gamboa, *Allen 4123* (MO). Between France Field and Cativa1, *Standley 30268* (US). PANAMÁ: Near Juan Días, *Killip 3341* (US). Río Tocumen, *Standley 29409* (US). Juan Díaz, *Standley 30508* (US). Between Matías Hernández and Juan Díaz, *Standley 32028, 32040* (both US).

Group 6. CALONYCTION

Calonyction Choisy, Mém. Soc. Phys. Genève. 6: 441. 1833. TYPE: *Ipomoea alba* L.
Ipomoea sect. *Calonyction* (Choisy) Griseb., Fl. Brit. W. Ind. 466. 1864.
I. subg. *Calonyction* (Choisy) Clarke, Fl. Brit. India 4: 197. 1883.

a. Sepals obtuse; corolla tube 6–10 cm long ..... 27. *I. macrantha*
aa. Sepals with abrupt prominent soft-spiny caudate tips; corolla tube 9–15 cm long ..... 26. *I. alba*

26. **Ipomoea alba** L., Sp. Pl. 161. 1753. LECTOTYPE: India, Rheede, Hort. Ind. Malabarii *t. 50, figs. 1 & 2.* 1692 (designated by Gunn 1972).

Ipomoea bona-nox L., Sp. Pl., ed. 2. 228. 1762. Nom nov. for *I. alba* L.
Calonyction aculeatum (L.) House, Bull. Torrey Bot. Club 31: 590. 1904.
Convolvulus aculeatus L., Sp. Pl. 155. 1753. TYPE: in herb. Pluk. (BM, not seen).

Vines; stems herbaceous at the tips, becoming woody at the base, smooth or often with short fleshy prickles, occasionally rooting near the nodes, glabrous. *Leaves* rounded ovate, entire or 3–5-lobed, 5–15 cm long, basally cordate, apically acuminate, glabrous. *Flowers* in 1- to several-flowered cymes, inflorescences and peduncles glabrous; sepals fleshy, ovate to elliptic, 10–20 mm long, apically

[6] A recently observed fruiting collection from Venezuela shows that *I. squamosa* is indeed a member of the *Eriospermum* group.

caudate at least on the outer sepals; corolla white with greenish nectar-guides, the tube 9–15 cm long, the rotate limb 8–10 cm broad. *Fruits* capsular, ovoid to subglobose, 2–3 cm long, 1–2 cm in diameter, with a 7–10 mm apiculus, mostly dark brown, glabrous; seeds dark brown to black, 8–10 mm long, glabrous.

Ipomoea alba usually flowers throughout the year with an apparent peak from November to January. It is pantropical in distribution.

Flowers of this species open rapidly at night and remain open until shortly after dawn. They are commonly visited by moths, particularly *Manduca sexta*, as they are adapted for moth pollination. The salverform, white corollas, and caudate sepals tips distinguish the species.

BOCAS DEL TORO: Near Chiriquí Lagoon, Water Valley, *Wedel 1523, 1645* (both MO, US). CANAL ZONE: Between Gorgona and Mamei, *Pittier 2244* (US). COCLÉ: 10 mi. E of Natá at Río Grande, *Godfrey 5227* (MO). DARIÉN: Río Tuira between Río Paya and Río Aspave, *Gentry 4428* (MO). Río Pirre, trail up river along Río Pirre from house of Bartata, *Kennedy 2871* (MO). Trail between Cana and Boca de Cupe, *Stern et al. 679* (US). Tucuti, Chepyana, *Terry & Terry 1398* (MO). HERRERA: Road from Chitré to Divisa, *Burch et al. 1358* (MO). PANAMÁ: Las Delicias, *Carleton 229* (US). Sabanas near Chepo, *Hunter & Allen 8* (MO).

27. **Ipomoea macrantha** Roem. & Schult. *in* L., Syst. Veg., ed. nov. 4: 251. 1819. TYPE: Based on *I. longiflora* R. Br.

Convolvulus tuba Schlecht., Linnaea 6: 735. 1831. TYPE: St. Thomas, *Ehrenberg* (not seen).
Ipomoea tuba (Schlecht.) G. Don, Gen. Syst. 4: 271. 1838
I. longiflora R. Br., Prodr. 1: 484. 1810, non Willd. (1809) TYPE: Australia, Queensland, *Brown 2741* (BM, not seen).
I. violacea L., Sp. Pl. 161. 1753. Typification recondite.

Vines; stems twining over low beach plants, perennial, glabrous. *Leaves* broadly ovate to reniform-ovate, 8–16 cm long, usually entire, cordate basally, acute to broadly acuminate apically, glabrous. *Flowers* usually solitary but occasionally 2–3 in a cymose inflorescence; sepals ovate to ovate-elliptic, 1.5–2.5 cm long, obtuse apically, glabrous; corolla white, the tube 6–8(–10) cm long, the limb campanulate to rotate. *Capsules* tardily dehiscent, ovoid to subglobose, 2–2.5 cm in diameter; seeds dark brown, pubescent with short stiff trichomes.

This pantropical species flowers from August to December.

Ipomoea macrantha is not closely related to the others in the *Calonyction* group; it is placed here for convenience. The actual affinity of the species is uncertain, but some data indicate possible alliance with *I. pes-caprae*. *Ipomoea macrantha* apparently represents the result of evolution onto a moth pollination syndromes convergent with the *Calonyction* group.

SAN BLAS: Beach E of Puerto Obaldía, *Croat 16915* (MO). Irandí, *Duke 6513* (MO). Isla Soskatupo, *Duke 8516* (MO). Isla Mosquito, *Duke 8871, 8930* (both MO). Guadia-Tupo, *Dwyer 6863, 6866* (both MO). Soskatupu, *Elias 1686* (MO). Near Ailigandí, *Lewis et al. 215* (MO). Around Puerto Obaldía, *Pittier 4391* (F, US).

Group 7. EXOGONIUM

Exogonium Choisy, Mém. Soc. Phys. Genève 6: 443. 1833. TYPE: *I. bracteata* Cav.
Ipomoea sect. *Exogonium* (Choisy) Griseb., Fl. Brit. W. Ind. 472. 1864.
I. subg. *Exogonium* (Choisy) Meisn. *in* Mart., Fl. Bras. 7: 221. 1869.

28. **Ipomoea purga** (Wender.) Hayne, Arzn. Gew. 12: 5. 33, 34. 1833.

Convolvulus purga Wender., Pharm. Centralbl. 1: 457. 1830. TYPE: Mexico, *Schiede* (not seen).
Exogonium purga (Wender.) Benth., Pl. Hartw. 46. 1840.

Vines; stems herbaceous, perennial, glabrous. *Leaves* ovate to broadly ovate, thin and chartaceous, 5–11 cm long, entire, cordate basally, acuminate or rarely acute apically, glabrescent. *Flowers* usually 1 or occasionally 2 per inflorescence; sepals unequal, oval, 4–9 mm long, obtuse and cuspidate, glabrous; corollas red-purple to rose-purple, the tube 7–8 cm long, the limb rotate to subcampanulate. *Fruits* not seen.

The species flowers in December. It ranges from southern Mexico to Panama.

While most other authors conclude that this species is not related to the *Exogonium* group, its actual affinity appears to lie there (Austin, unpublished data). The normally accepted concept of the *Exogonium* group utilizes the largely West Indian species as a focal point; these are actually most closely related to the *Eriospermum* group.

CHIRIQUÍ: 10.1 mi. N of David, *Lewis et al. 729* (MO).

Group 8. QUAMOCLIT

Quamoclit Moench, Meth. Bot. 453. 1794. TYPE: *I. coccinea* L.
Ipomoea sect. *Quamoclit* (Moench) Griseb., Fl. Brit. W. Ind. 472. 1864.
I. subg. *Quamoclit* (Moench) Clarke, Fl. Brit. India 4: 198. 1883.

a. Leaf blades divided more than halfway to the midrib with linear, acute lobes, the leaf appearing pinnately compound ..... 31. *I. quamoclit*
aa. Leaf blades entire, angled or 3–7-lobed, the lobes broad or narrow, obtuse, the leaf not appearing compound.
  b. Corolla limb deeply lobed, the lobes 7–15 mm long, the corolla yellow, often with purplish or violet markings ..... 30. *I. neei*
  bb. Corolla limb subentire or slightly lobed, the lobes small, less than 5 mm long, the corolla red or red-yellow ..... 29. *I. hederifolia*

29. **Ipomoea hederifolia** L., Syst. Nat., ed. 10. 925. 1759. TYPE: Based on Plumier, Pl. Amer. 81, *t.* 93, *f.* 2. 1756.

Quamoclit hederifolia (L.) G. Don, Gen. Hist. 4: 259. 1838.
Ipomoea coccinea auct. non L. (1753).
Quamoclit coccinea (L.) Moench var. *hederifolia* (L.) House, Bull. Torrey Bot. Club 36: 599. 1909.

Vines; stems slender and herbaceous, annuals, glabrous to sparsely pubescent. *Leaves* ovate to suborbicular, 2–15 cm long, entire, dentate, trilobate or rarely with 5 or 7 lobes, basally cordate, acute to acuminate apically, glabrous or remotely pubescent. *Flowers* in few- to several-flowered cymes or solitary; sepals oblong to elliptic, 1.5–3 mm long, apically obtuse or truncate, the outer sepals with a 1.6–6 mm long subterminal arista, glabrous; corollas red or red-yellow, 2.5–4.5 cm long, the tube 1–2 mm in diameter, the limb 1.8–2.5 cm in diameter. *Fruits* capsular, subglobose, 6–8 mm in diameter; seeds dark brown or black, pyriform, with usually 2 lines of short dark trichomes on the dorsal face.

Ipomoea hederifolia flowers from November to April. It is distributed through the southern United States, the West Indies, Mexico, Central America and South America; it is introduced into Malaysia and Africa.

This is the tropical counterpart of the apparently temperate *I. coccinea*. *Ipomoea hederifolia* is the only species in Panama with red to red-yellow salverform corollas with a subentire limb.

BOCAS DEL TORO: Isla Colón, *Wedel 2932* (MO, US). CANAL ZONE: Near Summit Gardens, *Correa & Dressler 660* (MO). Madden Dam, *Dwyer 2876* (MO). Between Farfan Beach and Palo Seco, *Hunter & Allen 436* (MO). Farfan Beach, *Lewis et al. 46* (MO). Red Tank to Pueblo Nuevo, *Piper 5771* (US). Sosa Hill, Balboa, *Standley 26408* (US). Between Fort Clayton and Corozal, *Standley 29200* (US). Farfan Beach, *Tyson & Blum 2609* (MO). CHIRIQUÍ: Quebrada Tuco, 9 mi. S of Puerto Armuelles, *Liesner 154* (MO). COCLÉ: Road to El Cope, *Burch et al. 1380* (MO). 1–5 mi. S of Antón, *Tyson & Blum 2562* (MO). LOS SANTOS: Near Las Tablas, *Burch et al. 1272* (MO). PANAMÁ: Sabanas near Chepo, *Hunter & Allen 9* (US). Panamá La Vieja, *Bro. Maurice 808* (US). Without locality, *Kennedy et al. 2018* (MO). Around Alhajuela, *Pittier 2341* (US). Near Matías Hernández, *Standley 28937* (US). Tumba Muerto Road, *Standley 29780* (US). Juan Díaz, *Standley 30502* (US). Between Las Sabanas and Matías Hernández, *Standley 31910* (US).

30. **Ipomoea neei** (Spreng.) O'Donell, Lilloa 29: 69. 1959.

Calboa vitifolia Cav., Icon. 5, *p. 51. t. 476.* 1799. TYPE: Mexico, Nayarit, *Nee*, (?MA, not seen).

Convolvulus neei Spreng., Syst. Veg. 1: 593. 1825. Nom. nov. for *Calboa vitifolia* Cav.

Quamoclit vitifolia (Cav.) G. Don, Gen. Hist. 4: 259. 1838.

Ipomoea peduncularis Bertol., Nov. Comment. Acad. Sci. Inst. Bonon. 4: 408. [Fl. Guat.] 408, *t. 38.* 1840. TYPE: Based on material from Guatemala cultivated in Italy. (not seen).

I. hartwegii Meisn. *in* Mart., Fl. Bras. 7: 220. 1869, non Benth. (1839). TYPE: Guatemala, *Hartweg 603* (not seen).

Lianas; stems woody, branched, striate or angular, glabrous. *Leaves* ovate, subtrilobate, subentire, 3(–5)-lobed, to 3-parted, 2.5–18 cm long, usually basally cordate but variable, acute to acuminate apically, glabrous or pubescent near the base. *Flowers* in 10–70-flowered cymes with few open at a time; sepals ovate to elliptic, 2.5–5 mm long, the outer sepals with a subterminal arista 2–5 mm long, glabrous; corollas yellow or violet or yellow with purple or violet markings 2.7–3.5 cm long with a 10–15-mm-long tube, 4–4.5 mm in diameter, the limb campanulate. *Fruits* capsular, subglobose, 7–9 mm in diameter; seeds black, pyriform, with yellowish patches of short trichomes.

This species flowers from December to April. It ranges from Mexico to Panama.

Perhaps a primitive member of the *Quamoclit* group, this is the only species with yellow flowers commonly marked with purple or violet.

CHIRIQUÍ: Bajo Mono, *Davidson 501* (F). Near Boquete, *Lewis et al. 410* (MO). Alto Lino, *Bro. Maurice 894* (US). Near El Boquete, *Maxon 5384* (US).

31. **Ipomoea quamoclit** L., Sp. Pl. 159. 1753. TYPE: LINN 219.1 (not seen; microfiche).

Convolvulus pennatus Desr. *in* Lam., Encycl. Méth. 3: 567. 1791. TYPE: Cultivated in Paris from East Indian material (not seen).

Quamoclit vulgaris Choisy, Mém. Soc. Phys. Genève 6: 434. 1833. New name for *Ipomoea quamoclit* L.
Quamoclit pennata (Desr.) Bojer, Hort. Maurit. 224. 1837.

Vines; stems slender, herbaceous, annual, glabrous. *Leaves* 1–9 cm long, ovate to elliptic in outline, deeply pinnatisect with 9–19 alternate or opposite pairs of linear lobes, glabrous. *Flowers* solitary or in 2–5-flowered cymes; sepals elliptic to oblong, 4–7 mm long, obtuse apically, with a 0.25–0.75-mm-long mucro, glabrous; corollas red or rarely white, 2–3 cm long. *Fruits* capsular, ovoid, 6–8 mm in diameter; seeds dark to black, with dark patches of short trichomes scattered somewhat irregularly.

This species flowers from June to January. Pantropical in distribution, it is cultivated in temperate zones. "Cundeamor."

An annual with deeply pinnatisect leaves, this species often appears in gardens. It is probably originally from Mexico, but was distributed to the Old World in early post-Colombian time.

BOCAS DEL TORO: Changuinola Valley, *Dunlap 232* (F, US). Isla Colón, *Wedel 506* (MO). Miraflores Bridge area, *Dwyer 1092* (MO). Farfan Beach, *Dwyer 6800* (MO). Barro Colorado Island, *Ebinger 202* (MO). Balboa Heights, *Killip 3059* (US). Balboa, *Standley 28544* (US). Near Fort Sherman, *Standley 31146* (US). CHIRIQUÍ: David, *Lewis et al. 741* (MO). Near Puerto Armuelles, *Woodson & Schery 825* (MO, US). PANAMÁ: Near Jenine, *Duke 3897* (MO). Around Alhajuela, *Pittier 2334* (US). Juan Díaz, *Standley 30595* (US). Las Sabanas, collector unknown (MO-1952163).

UNCERTAIN SPECIES

Ipomoea silvicola House, Bot. Gaz. (Crawfordsville) 43: 411. 1907.

This species was reported from Panama by House, but I have seen no material from there. Standley and Williams (Flora of Guatemala, Fieldiana: Bot. 24: 53. 1970) indicated that the specimen cited by House was probably collected in Guatemala.

Ipomoea ochracea var. *curtisii* (House) Stearn, Proc. Linn. Soc. Bot. 170: 145. (footnote). 1959.

Ipomoea curtisii House, Ann. New York Acad. Sci. 18: 257. 1908.

The type of this taxon was collected in Havana, Cuba (*Curtiss 562* GH, NY); another specimen was cited by House from Panama (*Cowell 166*, NY). Neither has been seen.

Ipomoea jamaicensis G. Don, Gen. Syst. 4: 278. 1838.

Hemsley (Biol. Centr.-Amer. 2: 388. 1882.) reported this species from Panama based on a collection by Grisebach. To my knowledge this species does not occur outside the West Indies. Perhaps Hemsley confused his specimen with *I. acuminata*, a mistake frequently made.

Ipomoea aristolochiaefolia (H.B.K.) G. Don, Gen. Syst. 4: 277. 1838.

This species supposedly ranges from Mexico to Argentina; no specimens have been seen from Panama although it is included in the key. The vegetative parts

of the species are similar to *I. tricolor*, but the small rose or violet flowers and delicate nature of the stems and leaves are distinctive.

Ipomoea parasitica (H.B.K.) G. Don, Gen. Syst. 4: 275. 1838.

Known from Mexico to northern South America, this species has apparently not been found in Panama. It is similar to *I. tricolor* but has smaller pubescent corollas.

Ipomoea wrightii Gray, Syn. Fl. N. Amer. 2(1): 213. 1878. TYPE: Texas, *Wright* (GH, holotype).

Cultivated from the southern United States to Argentina, this species may be found in Panama in the future. It can be recognized by the coiled, apparently climbing, peduncles.

Ipomoea tricolor Cav., Icones 3: *t. 208*. 1794.

This widely cultivated Mexican species is known as far south in Central America as Costa Rica, and it may be grown in Panama from imported seed, although no specimens have been seen. The name *I. violacea* has long been misapplied to this species, and most specimens are still determined with that name. It is recognized by the large blue flowers having a white throat and small sepals. Flowers of *Ipomoea acuminata* may also be blue at one stage of their development.

6. ARGYREIEAE

Argyreieae (Choisy) Choisy *in* DC., Prodr. 9: 325. 1845. TYPE: *Argyreia* Lour.

Argyreieae Choisy, Mém. Soc. Phys. Genève 6: 407. 1833, as "sectio."
Argyreieae (Choisy) Meisn. *in* Mart. Fl. Bras. 7: 204. 1869, as "subtribe."
Argyreiinae (Choisy) Peter *in* Engl. & Prantl, Nat. Pfl. 4(3a): 20. 1891.

10. ARGYREIA

Argyreia Lour., Fl. Coch. 134. 1790. TYPE: *A. obtusifolia* Lour.

Lettsomia Roxb., Fl. Ind. Ed. Carey and Wall. 2: 75. 1824. TYPE: Not chosen.
Moorcroftia Choisy, Mém. Soc. Phys. Genève 6: 431. 1833. TYPE: Not chosen.

Lianas, perennial. *Leaves* petioled, variable in size and shape, glabrous to pubescent. *Flowers* in axillary few- to many-flowered cymes; sepals 5, herbaceous to subcoriaceous, variable in shape and size, often hairy outside, slightly to much enlarged in fruit, in the latter case often red inside; corolla small to large, campanulate, funnelform or tubular, purple, red, pink, or white, the limb nearly entire to deeply lobed, the interplicae pubescent; stamens 5, included or exserted, the stigma biglobular. *Fruits* ellipsoid or globose, fleshy, leathery, or mealy berries, purplish, red, orange, or yellowish; seeds 4 or fewer, glabrous, rarely pilose at the hilum.

A genus of about 90 species in the Old World Tropics. One species is cultivated for ornament in the tropics and subtropics of the New World.

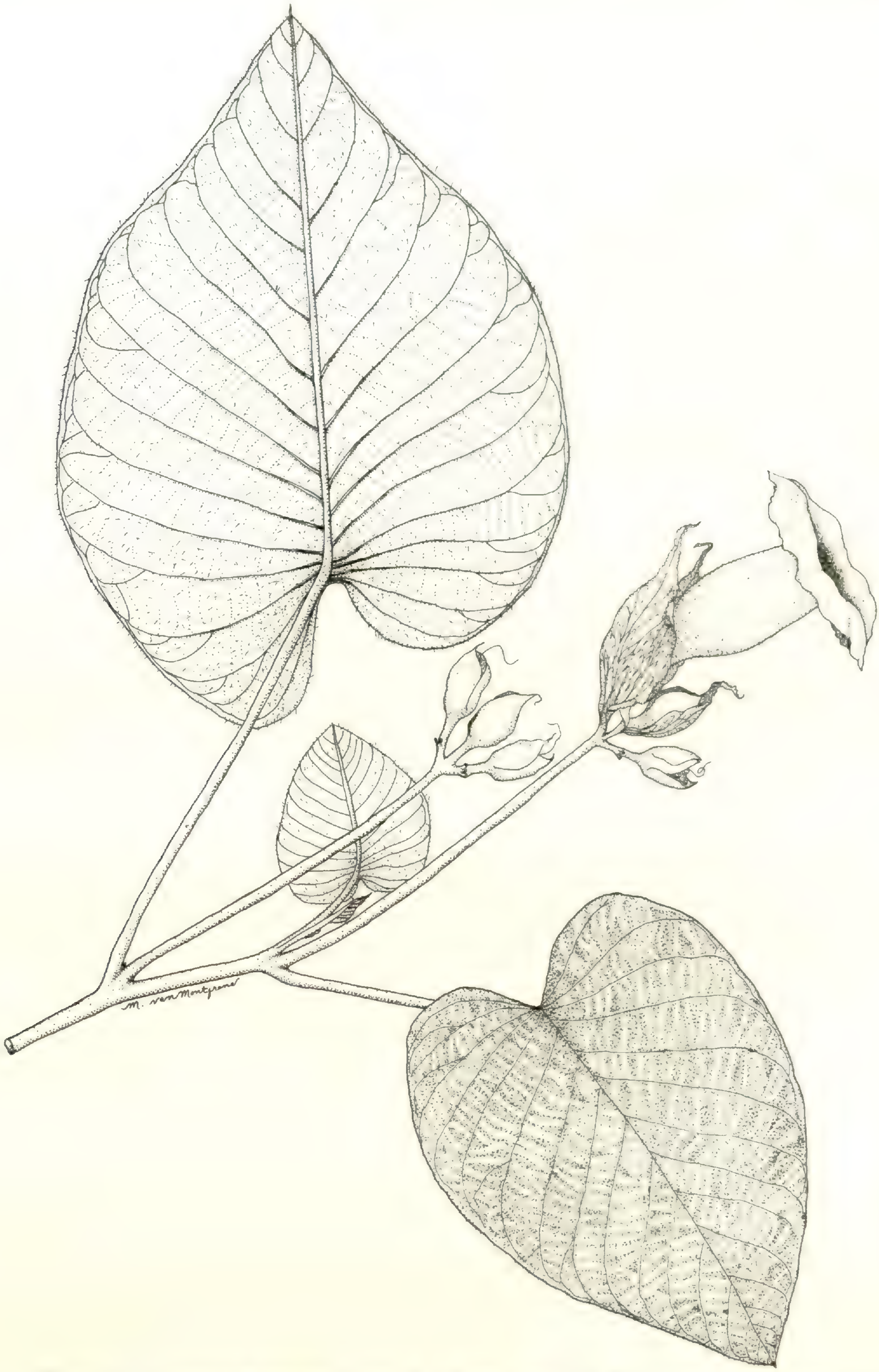

FIGURE 11. *Argyreia nervosa* (Burm. f.) Bojer, habit ($\times \frac{3}{5}$). [After *Avery 1338* Cultivated, Florida (FAU).]

1. **Argyreia nervosa** (Burm. f.) Bojer, Hort. Maurit. 224. 1837.—FIG. 11.

Convolvulus nervosus Burm. f., Fl. Ind. 48, *t. 20, f. 1.* 1768. TYPE: (not seen).
C. speciosus L. f., Suppl. 137. 1781. TYPE: Brazil, *Vandelli* (not seen).
Ipomoea speciosa (L. f.) Pers., Syn. Pl. 1: 183. 1805.
Lettsomia nervosa (Burm. f.) Roxb., Fl. Ind. Ed. Carey and Wall. 2: 78. 1824.
Argyreia speciosa (L. f.) Sweet, Hort. Brit. 289. 1827.
Rivea nervosa (Burm. f.) Hall. f., Bull. Herb. Boissier 5: 381. 1897.

Lianas; stems herbaceous toward the tips, woody at the base, younger branches densely white pubescent, glabrate with age. Leaves cordate, 18–27 cm long, apically acute to obtuse, entire. *Flowers* in cymes on long white tomentose peduncles; sepals ovate to broadly ovate, 1.5–2 cm long, white-tomentose; corollas with lavender limb and darker throat, 6–6.5 cm long, pubescent outside at least on the tube and interplicae. *Fruits* indehiscent, baccate, subglobose, 1–1.5 cm long; seeds dark to fairly light brown, glabrous.

This pantropical cultivar flowers in November.

CANAL ZONE: Cristobal, *Keenan 261* (US).

11. STICTOCARDIA

Stictocardia Hall. f., Bot. Jahrb. (Syst.) 18: 159. 1894. TYPE: *Convolvulus tiliifolia* Desr. = *Stictocardia campanulata* (L.) Merrill.

Vines to about 4 m in length, perennial; stems puberulent, glabrate, the older stems with exfoliating bark. *Leaves* petiolate, cordate, apically acuminate, entire, glabrate above and beneath but covered with small black glandular trichomes beneath. *Flowers* in 1–3-flowered axillary cymes; sepals subequal, orbicular with black glandular trichomes, becoming coriaceous and clasping in fruit; corolla funnelform, red or scarlet to purplish-red, the limb usually entire; stamens included, the filaments glandular-pubescent at the base, filiform above, the anthers oblong, pollen pantoporate, spheroidal, spinulose; ovary bilocular, the style longer than stamens, the stigma capitate, biglobose. *Fruits* indehiscent, thin-walled, surrounded by enlarged fleshy sepals, subspheroidal; seeds 4, ovoid, grayish brown, minutely pubescent.

A small genus of about 12 species widely spread in the tropics although apparently native to the Old World. The most widespread species, *Stictocardia campanulata*, is introduced as far north in the New World as southern Florida. This is the only species in Panama. The flowers of the genus are apparently adapted for bird pollination.

Literature:

Gunn, C. R. Notes on *Stictocardia campanulata* (L.) Merrill and S. *jucunda* (Thev.) C. R. Gunn (Convolvulaceae). Brittonia 24: 169–76. 1972.

1. **Stictocardia campanulata** (L.) Merrill, Jour. Sci. Phil. Bot. 9: 133–134.—FIG. 12.

Ipomoea campanulata L., Sp. Pl. 1: 160. 1753. LECTOTYPE: India, Adamboe, Hort. Ind. Malabar. 16: 115. *t. 56.* 1692

FIGURE 12. *Stictocardia campanulata* (L.) Merrill.—A. Habit ($\times$ 3/5).—B. Fruit ($\times$ 3/5).—C. Seed, ventral view ($\times$ 1 1/5).—D. Seed, dorsal view ($\times$ 1 1/5). [A after *Standley 26227* (US). B–D after *Macbride 2614* (US).]

Convolvulus tiliafolius Desr. *in* Lam., Encycl. Méth. 3: 544. 1791. TYPE: Mauritius, *Comerson* (P, not seen).
Stictocardia tiliaefolia (Desr.) Hall. f., Bot. Jahrb. (Syst.) 18: 159. 1894.

Lianas; stems herbaceous at the tips becoming woody with age, puberulent but glabrate with age. *Leaves* cordate to cordate-ovate, 8–25 cm long, basally cordate, apically acute to short-acuminate, glabrate above and beneath. *Flowers* mostly solitary in leaf axils, occasionally cymose and 1–4-flowered; sepals suborbicular, 1–2 cm long, puberulent to glabrate; corollas crimson outside, striped inside with yellow to yellow-red bands, funnelform, 5–8 cm long. *Fruits* globose, 2.5–3 cm in diameter, indehiscent, surrounded by the accrescent calyx which eventually disintegrates leaving the vascular framework; seeds obovoid, greyish-brown, pubescent with minute trichomes.

This widely cultivated pantropical species flowers from November to January. The crimson flowers make the species attractive and distinctive.

PANAMÁ: Panama City, *Macbride 2614* (F, US). Bella Vista, *Standley 25338* (US). Near Punta Paitilla, *Standley 26227* (US), *30804* (MO, US).

12. TURBINA

Turbina Raf., Fl. Tellur. 4: 81. 1838. TYPE: *T. corymbosa* (L.) Raf.

Legendrea Webb & Berth., Hist. Nat. Îles Canaries, Bot. 3, 2: 26. 1844. TYPE: *L. mollissima* Webb & Berth. = *Turbina corymbosa* (L.) Raf. var.

Lianas, often high climbing, pubescent or glabrous. *Leaves* petiolate, cordate and entire. *Flowers* white, greenish, pink, or crimson, solitary or on many-flowered axillary or terminal inflorescences; sepals ovate or lanceolate, the outer ones sphaecelate, often unequal, accrescent in fruit; corolla funnelform or salverform; the filaments filiform with glandular-pubescent, dilated bases, pollen pantoporate, spheroidal, spinulose; ovary glabrous, 2-locular, the style single, the 2 stigmas globose. *Fruits* indehiscent, dry, mostly ligneous to subligneous, ellipsoid to subglobose, 1-locular, mostly 1-seeded; the seeds pubescent.

This is a genus of about 12 species in the tropics of New and Old World. Species are largely included on the basis of having indehiscent ovoid-oblong or ellipsoid fruits, usually with a single seed. The genus is probably not a natural taxon and needs study.

a. Flowers 2.5–3 cm long, campanulate-funnelform, white with a dark brown or purplish throat, trichomes on filament base orange; leaves mostly glabrous, rarely puberulent ..... 1. *T. corymbosa*
aa. Flowers 6–7 cm long, funnelform, reddish to lilac or rarely white, trichomes on filament base white to reddish; leaves mostly pubescent at least on lower surface ..... 2. *T. abutiloides*

1. **Turbina corymbosa** (L.) Raf., Fl. Tellur. 11: 81. 1836.

Convolvulus corymbosa L., Syst. Nat., ed. 10. 923. 1759. TYPE: Based on Plumier, Pl. Amer. 78. *t.* 89. *f.* 2.
Rivea corymbosa (L.) Hall. f., Bot. Jahrb. (Syst.) 18: 157. 1893.
Convolvulus sidaefolia H.B.K., Nov. Gen. Sp. Pl. 3: 99. 1818. SYNTYPES: Canary Islands; Venezuela, *Humboldt & Bonpland* (not seen).
Ipomoea sidaefolia (H.B.K.) Choisy, Mém. Soc. Phys. Genève 6: 459. 1833.

Lianas; stems herbaceous at the tips, woody at the base, glabrous to glabrate. *Leaves* cordate-ovate, 4–10 cm long, apically acute to shortly acuminate, glabrous or rarely pubescent. *Flowers* in axillary or terminal thryses; sepals oblong, 8–12 mm long, glabrous; corollas white with a dark brown to purplish area in the lower part of the tube, 2.5–3 cm long. *Fruits* indehiscent, ovoid-oblong, 1–1.5 cm long; seeds one, rarely two, per fruit, pubescent with short trichomes.

This species flowers in February and March. It occurs from Mexico to Panama, in the West Indies, southern Florida and South America. It is introduced into the Philippines.

The white flowers with a brown or brown-purple base inside the tube and the small, one-seeded fruits make the species distinctive.

BOCAS DEL TORO: Talamanca Valley, *Carleton 119* (US). CANAL ZONE: Empire to Mandinga, *Piper 5459, 5517* (both US). DARIÉN: Hydro Camp on Río Mortí, *Duke 15410* (MO). PANAMÁ: Cerro Campana on road to Su Lin, *Kennedy et al. 2026* (MO). Between Savanas and Río Yguana, *Macbride 2641* (F, US).

2. **Turbina abutiloides** (H.B.K.) O'Donell, Lilloa 23: 505, *pl. 11.* 1950.

Convolvulus abutiloides H.B.K., Nov. Gen. Sp. Pl. 3: 83. 1819. TYPE: Ecuador, ? *Bonpland* (not seen).
Ipomoea abutiloides (H.B.K.) G. Don, Gen. Syst. 4: 273. 1838.
Rivea abutiloides (H.B.K.) Hall. f., Bot. Jahrb. (Syst.) 18: 158. 1893.

Lianas; stems more or less woody throughout, appressed-tomentose throughout, the extremities densely so. *Leaves* ovate to ovate-cordate, 3–9 cm long, basally cordate, apically acute to acuminate, glabrescent to densely pubescent below. *Flowers* in axillary or subterminal compound cymes; sepals subequal, the exterior sepals elliptic to obovate-elliptic, 14–20 mm long and often with a few trichomes at the apex or on the back, the interior sepals elliptic, obtuse to subacute, rarely emarginate, mostly glabrous; corollas reddish to lilac or rarely white, 6–7 cm long, the interplicae pubescent. *Fruits* indehiscent, ovoid, 14–17 mm long, 6–7 mm in diameter, apiculate, subtended by the accrescent sepals; seeds ellipsoid, 9–10 mm long, dark brown, finely pubescent with short trichomes.

This species flowers from October to December. It occurs in Ecuador, Colombia, Venezuela and Panama.

COCLÉ: Road to El Cope, *Correa 405* (MO). LOS SANTOS: Headwaters Río Pedregal, *Lewis et al. 2949* (MO). 12 mi. S of Macaracas, *Tyson et al. 3076* (MO).

7. DICHONDREAE

Dichondreae (Choisy) Choisy *in* DC., Prodr. 9: 325. 1845. TYPE: *Dichondra* Forst.

Dichondraceae Dumortier, Anal. Fam. 20, 24, 1829.
?Wilsonieae Hall. f., Bot. Jahrb. (Syst.) 16: 568. 1893. TYPE: *Wilsonia* R. Br.
Dichondroideae Roberty, Candollea 14: 22. 1952.
?Wilsonioideae Roberty, Candollea 14: 23. 1952.
Nephrophylleae Roberty, Candollea 14: 23. 1952. TYPE: *Nephrophyllum* A. Rich.
?Wilsoniinae (Hall. f.) Ooststr., Fl. Males. 4: 389. 1953.
Dichondrinae (Choisy) Ooststr., Fl. Males. 4: 389. 1953.

13. DICHONDRA

Dichondra J. R. & G. Forster, Char. Gen. Pl. 39, *pl. 20.* 1776. TYPE: *D. repens* Forster.

Herbs with slender glabrous or pubescent stems which are mostly repent. *Leaves* cordate-orbicular to reniform, small, entire, with long petioles. *Flowers* inconspicuous, small, axillary, greenish-yellow, solitary and pedicellate; sepals subequal, distinct, mostly spathulate; corolla broadly campanulate, deeply 5-lobed, the lobes induplicate; stamens shorter than the corolla, the filaments subulate or filiform, the anthers cuniform, the pollen 3-colpate; ovary bilobate, the lobes distinct or basally united, 2-locular, biovulate, styles 2, attached between the ovary lobes and appearing almost gynobasic, filiform, the stigmas capitate. *Fruits* capsular or utriculate, 2, membranaceous, usually 1-seeded, irregularly bivalvate or indehiscent; seeds subglobose, smooth, the cotyledon oblong-linear, 2-plicate.

A small genus of about 12 closely allied species, *Dichondra* is pantropical in distribution.

Literature:

Tharp, B. D. & M. C. Johnston. Recharacterization of *Dichondra* and a revision of North American species. Brittonia 13: 346–360. 1961.

1. **Dichondra sericea** Swartz, Prodr. Veg. Ind. Occ. 54. 1788.

D. repens var. *sericea* Choisy *in* DC., Prodr. 9: 451. 1845.

No specimens of *Dichondra* have been seen from Panama, but this species occurs in Guatemala, Costa Rica and Venezuela. It is to be expected in Panama.

8. CUSCUTEAE

Cuscuteae (Choisy) Choisy *in* DC., Prodr. 9: 325. 1845. TYPE: *Cuscuta* L.

Cuscuteae Choisy, Mém. Soc. Phys. Genève 6: 497. 1833, as "sectio."
Cuscuteae Baillon, Hist. Pl. 10: 330. 1891, as "série."
Cuscutoideae (Choisy) Peter *in* Engl. & Prantl, Nat. Pfl. 4(3a): 13, 37. 1891.
Cuscutaceae Dumortier, Anal. Fam. Pl. 20. 1829.

14. CUSCUTA

Cuscuta L., Sp. Pl. 124. 1753; Gen. Pl., ed 5. 60. 1754. TYPE: *C. europaea* L.

Vines without chlorophyll; the stems twining, filiform, yellow or orange or rarely greenish, attached to host plants by haustoria; roots withering and absent from mature plants. *Leaves* reduced to minute scales. *Inflorescences* cymose, composed of small whitish flowers; calyx gamosepalous, 5-lobed, the sepals rarely almost free; corolla urceolate or campanulate, the 5 lobes various, usually with basal scale-like appendages inside opposite the stamens, forming a corona; the pollen 3-colpate; ovary 2-locular, locules biovulate, styles 2, distinct or rarely united, terminal, the stigmas capitate to linear. *Fruit* capsular or circumscissle near the base; the seeds (1–3)–4, smooth or roughened.

A genus of 140–150 species of worldwide distribution. The genus is not well represented in Panama, only one species being found.

Literature:

Yuncker, J. G. Revision of the North American and West Indian species of *Cuscuta*. Univ. Illinois Biol. Monog. 6: 1–142. 1921.

———. The genus *Cuscuta*. Mem. Torrey Bot. Club 18: 113–331. 1932.

———. *Cuscuta*. N. Amer. Fl., ser. 2. 4: 1–51. 1965.

1. **Cuscuta woodsonii** Yuncker *in* Woods. & Seibert, Ann. Missouri Bot. Gard. 26: 305. 1939. TYPE: Panama, *Woodson et al.* 950 (US, holotype; MO, isotype).

Stems coarse. *Flowers* membranous or somewhat fleshy, 4 mm long from the base to corolla sinuses, subsessile in scattered few-flowered clusters; sepals orbicular-ovate, broadly overlapping, obtuse, fleshy in the median and lower parts, thin toward the edges, loose around the corolla, not reaching the corolla sinuses; corolla campanulate, the lobes about as long as the tube, broadly ovate, obtuse, basally auriculate and overlapping, upright to spreading; filaments subulate, flattened, longer than the anthers; infrastaminal scales prominent, reaching the anthers, oblong, apically fringed and sparingly fringed along the sides. Capsules depressed-globose, to 6 mm in diameter, the interstylar aperture large, surrounded by the withered corolla and circumscissile when mature; seeds ovoid, 2.5 mm long, the hilum oblong, oblique.

This species flowers from June to July. It is known only from Panama.

Cuscuta trichostyla Engelm. was reported from Panama by Yuncker (1932) in error. This species is actually a Brazilian plant erroneously attributed to Central America. The type collection was made in Parana, Brazil, by Tweedie (MO) and incorrectly ascribed to Panama.

Cuscuta corymbosa var. *grandiflora* is known from Costa Rica and Colombia, but no specimens from Panama have been seen.

CHIRIQUÍ: Volcán de Chiriquí, *Davidson 967* (US). Near Casita Alta, *Woodson et al. 950* (MO, US). Potrero Mulato, *Woodson & Schery 454* (MO).

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Angiosperm Biogeography and Past Continental Movements

Peter H. Raven and Daniel I. Axelrod

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"In the present paper, we examine the distributions of flowering plants, present and past, and attempt to interpret them in the light of newly available geological evidence. Although the field is vast, . . . we believe that an overview of angiosperm distributions in the light of geological history as now suggested by plate tectonic theory will be useful in suggesting new hypotheses and new directions for future research."

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BIOGEOGRAPHY: THE TWENTY-FIRST SYSTEMATICS SYMPOSIUM

GERRIT DAVIDSE[1]

The following eight papers were presented at the Twenty-first Annual Systematics Symposium held in the Lehmann Building of the Missouri Bontanical Garden, 18–19 October 1974. Symposium participants included a wide array of biologists and students from 27 states and Canada. Expenses were in part defrayed by the National Science Foundation (Grant GB-36049): their long-time support of the Systematics Symposium is gratefully acknowledged. The format of the Symposium followed the well established pattern of informal conversation and discussion on Friday evening, 18 October, followed by a formal program of papers, including discussion periods, on Saturday, 19 October. Dr. Richard A. Howard, Arnold Arboretum, gave the after-dinner talk and his presentation is published at the end of the Symposium. Dr. Peter H. Raven, Director of the Missouri Botanical Garden, served as moderator and his summary and concluding remarks are presented at the end of the invited papers.

The development over the last decade of the theory of plate tectonics and its subsequent nearly universal acceptance has been an enormous stimulus to a worldwide renewed interest in the study and reappraisal of biogeography at all levels. The realization that the relationship between the continents and ocean basins is a dynamic one has necessitated the reshaping of biogeographical theory, principles, explanations, and procedures along similar dynamic lines. With the resurgence of interest in the topic, it was clear that a Symposium on biogeography would be a timely one.

Because of the limited time of the Symposium and the vastness of the subject matter, it was self-evident that a broad review of biogeography could not be attempted and the alternate approach of presenting highlights of types of biogeographical studies was taken. Both zoologists (Cracraft, Edmunds and McKenna) and botanists (Axelrod, Savile, Thorne and Wolfe) presented papers. The need for a solid theoretical perspective for historical biogeography is stressed

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by Cracraft, and in a similar vein Edmunds stresses the need to increase the rigor of basic principles and methodology in biogeography, illustrating his phylogenetic approach from his work with mayflies. A historical approach to answer specific problems is taken in the papers by Axelrod, McKenna, and Wolfe. Axelrod and Wolfe discuss the evolution of vegetation patterns in the northern hemisphere and McKenna presents geological and paleontological evidence for continuous land areas around the north end of the Atlantic Ocean. Savile and Thorne stress the biogeography of extant organisms. Savile demonstrates the value of coevolutionary studies of parasites and their hosts in understanding the geographical patterns of such organisms, and Thorne illustrates how incongruous distributional patterns may suggest reinterpretations of the relationships between major taxa of plants.

HISTORICAL BIOGEOGRAPHY AND EARTH HISTORY: PERSPECTIVES FOR A FUTURE SYNTHESIS[1]

JOEL CRACRAFT[2]

It has now become almost cliché to speak of the revolution in the earth sciences and its ensuing revitalization of biogeography. Certainly much of the biogeographic literature of the past several years has been produced in response to our rapidly changing knowledge of earth history. While we can applaud the recent advances in biogeography, it is questionable whether we should be overly optimistic about obtaining a synthesis of the geographical history of plants and animals on the one hand and earth history on the other. I say this not because a synthesis is impossible, but because a synthesis will only be produced when the majority of workers reach some general agreement on the theoretical bases for reconstructing the historical biogeography of organisms. The reason for this statement is simple—observations are theory-laden. Indeed, individual theoretical biases—some of which we may not be consciously aware—determine the kinds of data we collect and thus the manner in which we order those data. If biogeographers differ in their theoretical approaches, then it can be expected that the observations are likely to differ as well as the interpretations. That this is a major problem in biogeography today is easily demonstrated by comparing the papers of Darlington, Brundin, and others among zoologists, and Thorne, Smith, Raven, Axelrod, Croizat, or van Steenis among botanists.

I believe most biogeographers would subscribe to the belief that the biotic and geologic worlds have evolved together, and that major distributional patterns of both plants and animals should be similar to each other and relate to major historical changes in geography and climate in a parallel manner. If this is true, then a synthesis would appear possible, and it would seem useful to begin an examination of the factors necessary to affect it. The purpose of this paper is, first, to examine the various theoretical approaches to historical biogeography and attempt to resolve some of the conflicts among them, and second, to outline several biogeographical patterns in which the distributional history of plants and animals seems consistent with earth history. One of the themes of this paper is that a lack of theoretical perspective has prevented us from seeing some of these common patterns. It is not my purpose to provide the synthesis I have been talking about; that would take far more space than is available here. Rather, I wish to discuss ideas that might facilitate zoologists and botanists alike finding some common ground in the analysis of historical biogeography.

THEORETICAL APPROACHES TO HISTORICAL BIOGEOGRAPHY

As noted above, historical biogeography is in a transitional period in which many, if not most, biologists no longer look at the world's continents and oceans

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[1] This paper was written during the tenure of a grant from the National Science Foundation (GB-41089); their support is gratefully acknowledged.

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from a stabilist point of view but rather from that of a mobilist. The theoretical foundations of historical biogeography are also in a state of flux, and several models or methods of analysis have been proposed as being useful for interpreting biogeographic history.

A major controversy exists, on the one hand, between a group of workers who have attempted to outline what they believe is a logically consistent methodology for reconstructing the geographic history of plants and animals and, on the other hand, the critics of that methodology. The theoretical approach developed by the former workers involves the construction of hypotheses about the phylogenetic relationships of the organisms in question and the subsequent inference of their geographic relationships (Hennig, 1966*a*, *b*; Brundin, 1966, 1972*a*; Nelson, 1969; Cracraft, 1973*a*). The opponents of this theory focus their criticism on the phylogenetic model of these workers and advocate a biogeography which does not have a precise deductive link with phylogenetic hypotheses, *e.g.*, Darlington, 1957, 1965, 1970); this has been termed the common-sense approach to biogeography (Rotramel, 1973). The crux of the controversy between the two schools of thought is whether biogeographic history is deducible from phylogenetic history and (1) if it is, what will be the logical steps in inferring biogeography from phylogeny, and (2) if it is not, how is biogeographic history then to be reconstructed? Both these theoretical approaches show some similarities in that they usually look upon biogeography in terms of centers of origin and dispersal from these centers, a conceptual framework in use since the time of Darwin. A third theoretical approach to biogeography de-emphasizes the concepts of centers of origin and dispersal and attempts to analyse distribution patterns in terms of subdivision (vicariance) of ancestral biotas (Croizat, 1962; see particularly Croizat *et al.*, 1974). A discussion of these three approaches will comprise this section of the paper.

APPROACH NO. 1: THE PHYLOGENETIC SYSTEMATIC THEORY OF BIOGEOGRAPHY

The phylogenetic systematic theory of historical biogeography is simply stated. From an hypothesis of phylogenetic relationships and knowledge of the distributions of the species under consideration, one can infer the distribution of the ancestral (hypothetical, unknown) species of each lineage in the phylogeny. This process completed, one has constructed a biogeographic hypothesis about the centers of origin and direction of dispersal that is most parsimonious for the given phylogenetic hypothesis (see Nelson, 1969, for a detailed discussion of the reasoning involved). Thus, if one considers four taxa (A–D) assumed to be related as in Fig. 1, we first ask what were the distributions of the ancestral species (open circles). Two alternatives are presented in Fig. 1, and it should be apparent that one, Fig. 1A, is more parsimonious than the other. In the former the center of origin is in Asia with subsequent dispersal to North America, whereas in the latter the origin is postulated as being in North America with dispersal to Asia. Parsimony is applied on the basis of the number of dispersals (dotted circles) required by each hypothesis. It is evident that hypotheses about the distributions of ancestral species are not influenced by the taxa A–D being fossil, extant, or a combination of both.

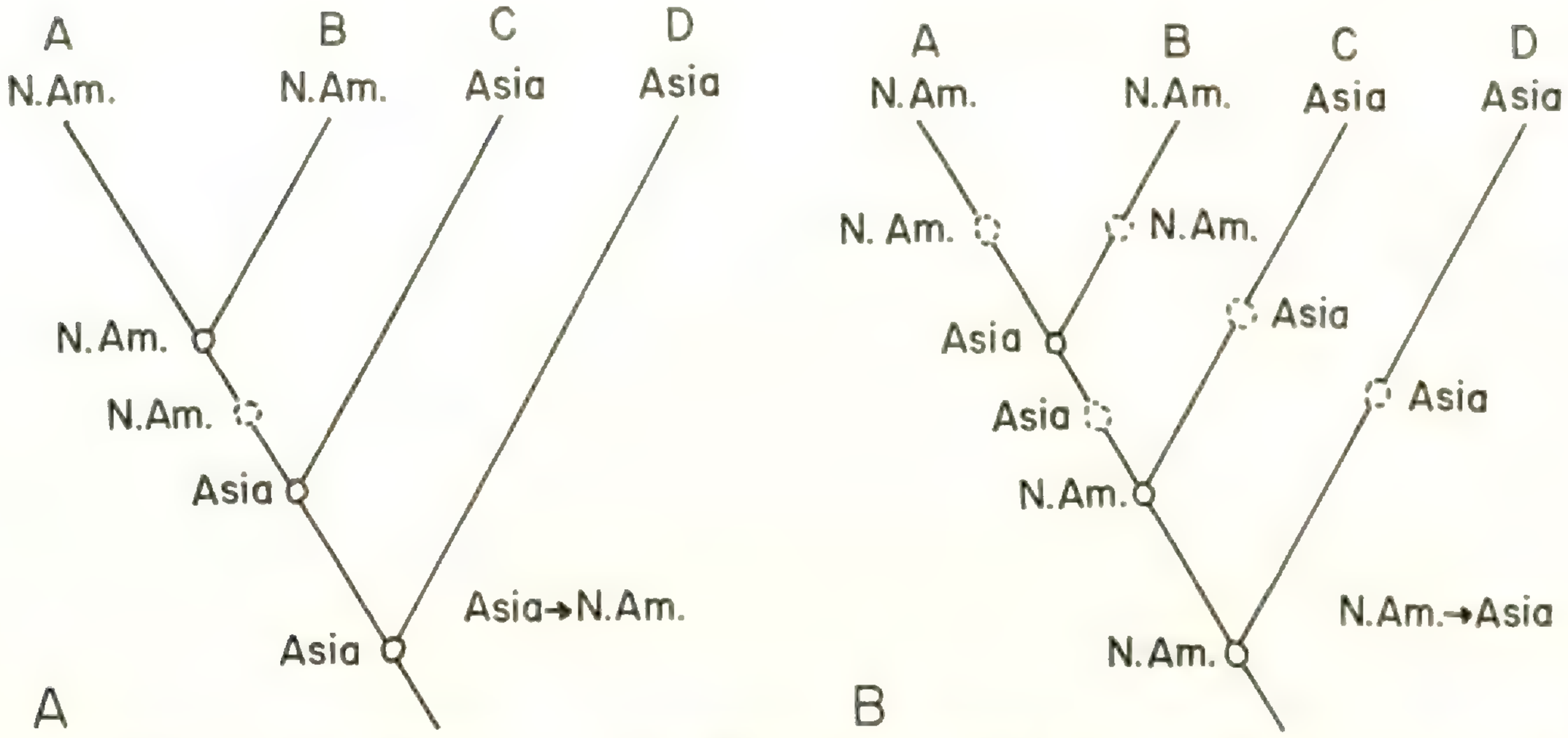

FIGURE 1. Two biogeographic hypotheses about four taxa (A–D) whose relationships and distributions are as shown. Geographic distributions of ancestral species (open circles) are postulated as are dispersal events (dotted circles). In A distributions of ancestral species are determined using the reasoning of Hennig-Brundin; the center of origin is postulated to be Asia with one dispersal to North America. In B an admittedly extreme biogeographic hypothesis is constructed to illustrate the concept of choosing among hypotheses on the basis of parsimony; thus hypothesis A is to be preferred. See text and Nelson (1969).

It should be emphasized that this methodology describes a mode of reasoning applied to a phylogeny that *is considered as given.* Of course, the phylogenetic relationships of taxa A–D may not be those portrayed in Fig. 1 (there are 13 additional possibilities), but that is another matter for discussion and is not directly relevant to the *reasoning* used to construct biogeographic hypotheses. If this mode of inference is followed, the center of origin is postulated to be located in the area where the phyletically primitive species are distributed.[3] This is simply a consequence of the reasoning—a methodological principle—and does not follow from any intuitive or prior belief that primitive species *must* have remained, at the center of origin of the group as a whole. I will return to this point shortly.

APPROACH NO. 2: CLASSICAL EVOLUTIONARY BIOGEOGRAPHY

This is the approach often associated with the names of Darwin, Matthew, Simpson, Darlington, and Mayr. The principles of this school are rather loosely formulated but might be listed as follows (see especially Darlington, 1957: 31–35):

1. The center of origin of a taxon is that area showing the greatest species and generic diversity. Darlington (1957: 31–32) notes that this criterion is more reliable for dominant, expanding groups than for those that are declining in diversity or area.

2. The degree of differentiation of a group is roughly proportional to the length of time that group has occupied the area in question.

---

[3] By "phyletically primitive" species I refer to those species which have branched off earliest within a lineage; this concept is independent of any considerations of whether these species are primitive or advanced morphologically (see discussion later in text).

3. The area occupied by a group is more or less proportional to the age of the group.

4. Distributions of peripheral groups that are more nearly continuous with the distribution of the "central" populations are probably younger than those peripheral populations with widely separated (relict) distributions.

5. Related, competing, or "associated" taxa tend to arise in the same areas as the taxon under consideration. Darlington (1957: 33) recognizes two corollary principles: (a) "much differentiated forms . . . isolated from the main range of their groups . . . are often not immigrants but relicts persisting where the first groups were once numerous but have become replaced." (b) "if groups arise in certain places because of favorable conditions there, they are likely to begin recession in the same places because of the rise of later families responding to the same conditions."

6. The distributions of primitive forms are not trustworthy for recognizing centers of origin.

7. Fossils provide the best clues for biogeography if the record is "adequate." Simpson (1965: 77) also notes that if the record is "fairly complete, the historical events can be followed with considerable objectivity and little inference."

The above points roughly define the working methods of classical evolutionary biogeography. It must be stressed that few biogeographers advocating this approach would suggest that any one of these methods is infallible; more often, they might say that, taken together, these rules should enable a reconstruction of biogeographic history, but, taken alone, the rules may be misleading. Nor should it be assumed that all evolutionary biogeographers would adhere to each of the above working principles.

Comments on the Conflict between Phylogenetic Systematic Biogeography and Classical Evolutionary Biogeography.—A major critique of the phylogenetic systematic theory outlined earlier was presented by Darlington (1970). Most of Darlington's article was directed toward criticizing a specific model of phylogeny reconstruction advocated by Hennig and Brundin. At this time we need not be concerned with this issue since Brundin (1972*a*, 1972*b*) has offered a rebuttal; rather, attention will be directed to the biogeographic aspects of the criticism.

I begin by suggesting that some of the differences between these two schools of thought may not be as deep as first realized. Both, I believe, accept the notion that knowledge of phylogeny is of considerable importance in reconstructing biogeographic history. While it is true that they may be using quite different phylogenetic models—that is, different methods of phylogeny reconstruction (Cracraft, 1974*a*)—their general picture of how phylogeny relates to dispersal history is sometimes very similar.

The notion that as organisms evolve they disperse over the globe is assumed by both schools. A concept of this dispersal was presented by Darlington (1959: 308, figs. 1–2) and is shown here in Fig. 2. One can draw a phylogeny of a group of organisms (Fig. 2A), and if that phylogeny is transposed to a map so that the organisms occupy their current (or past) distributions (Fig. 2B), then a dispersal history is effectively created. A somewhat more formal way of postulating that history is shown in Fig. 2C. The conclusion which one might draw from these

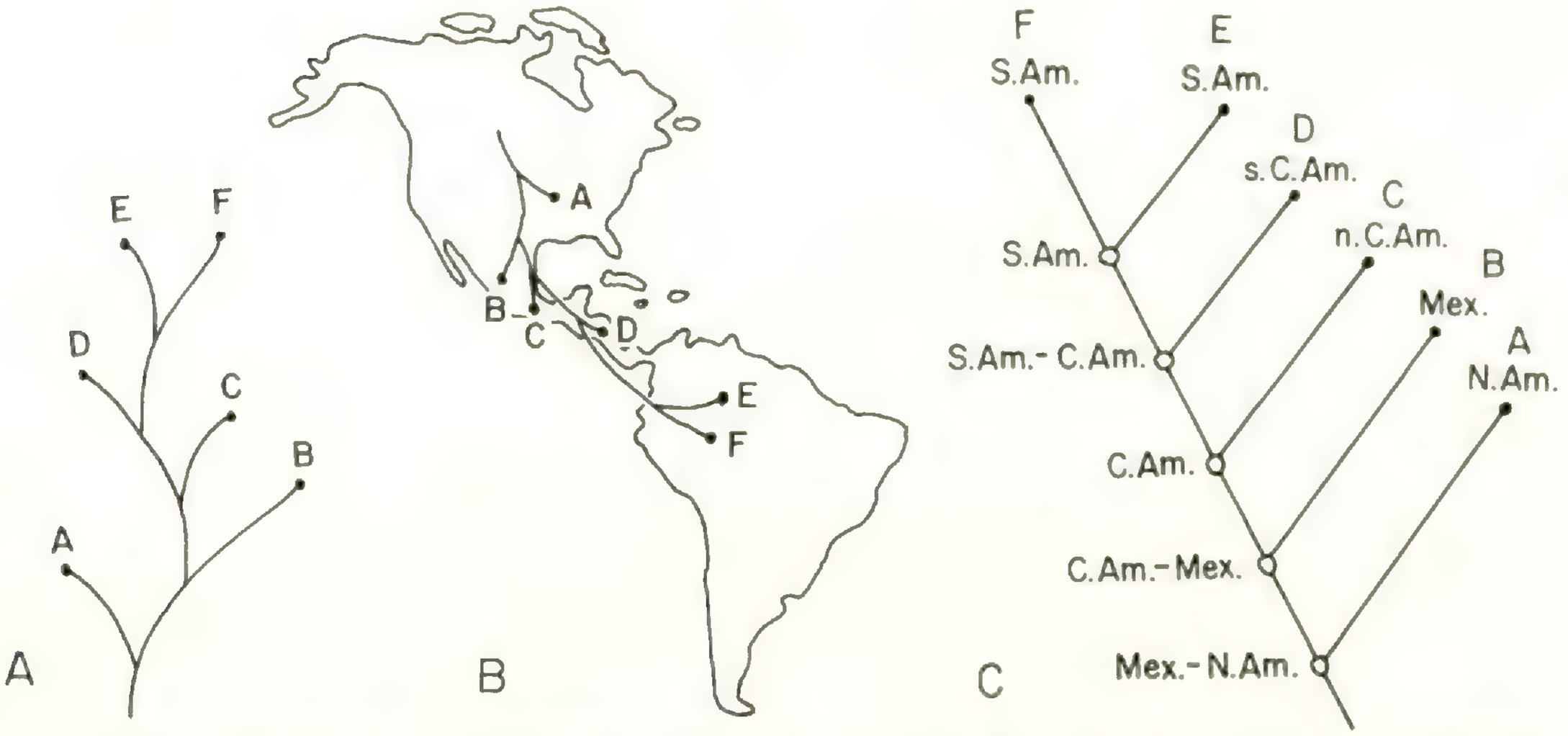

FIGURE 2. The link between phylogeny and dispersal as modified from a discussion of Darlington (1959). In A a phylogeny is presented for six taxa (A–F); this is typical of a phylogenetic scheme accepted by most workers. In B the phylogeny is superimposed on a geographic map; the reader will note the similarities to the example of Darlington (1959:308, fig. 2). It is clear from B that dispersal was from North to South America. In C this biogeographic hypothesis is formalized and the distributions of ancestral species (open circles) are postulated. One group of biogeographers (Darlington) advocates A–B, whereas another (Hennig-Brundin) advocates C; the differences are minimal.

workers' discussions is that if Darlington, Hennig, or perhaps most other biogeographers were presented with an agreed-upon phylogeny, all might arrive at similar concepts of dispersal history. Differences would probably develop depending on the degree to which one or more individuals might want to depart from parsimony in choosing among alternative hypotheses. Indeed, one point which will be developed below is that this departure from parsimony may be a major cause of the misunderstanding among these workers.

Classical evolutionary biogeographers have raised a number of issues which purportedly directly invalidate the methodology of phylogenetic systematic biogeography or which are thought to provide a more reliable basis for reconstructing biogeographic history.

The Problem of Primitive Groups.—The notion that centers of origin can be identified by location of "primitive" groups has been greatly misunderstood by many biogeographers. In fairness, it should be said that advocates of the phylogenetic systematic theory have themselves not fully appreciated the problems involved and have contributed to this misunderstanding. One cause of the confusion is definitional, that is, what is meant by a "primitive" group. Darlington (1970: 10–11), for example, argued against Brundin's (1966: 56) statement that ". . . within the total distribution area of a group the species possessing the most primitive characters are found within the earliest, those with the most derivative characters within the latest occupied part of the area." Brundin here and elsewhere (1972*a*: 73–74) uses primitive in the sense of "morphologically primitive" instead of "phyletically primitive" and there may not be a precise relationship between the two (Fig. 3). To my knowledge Brundin has not used "primitive" in

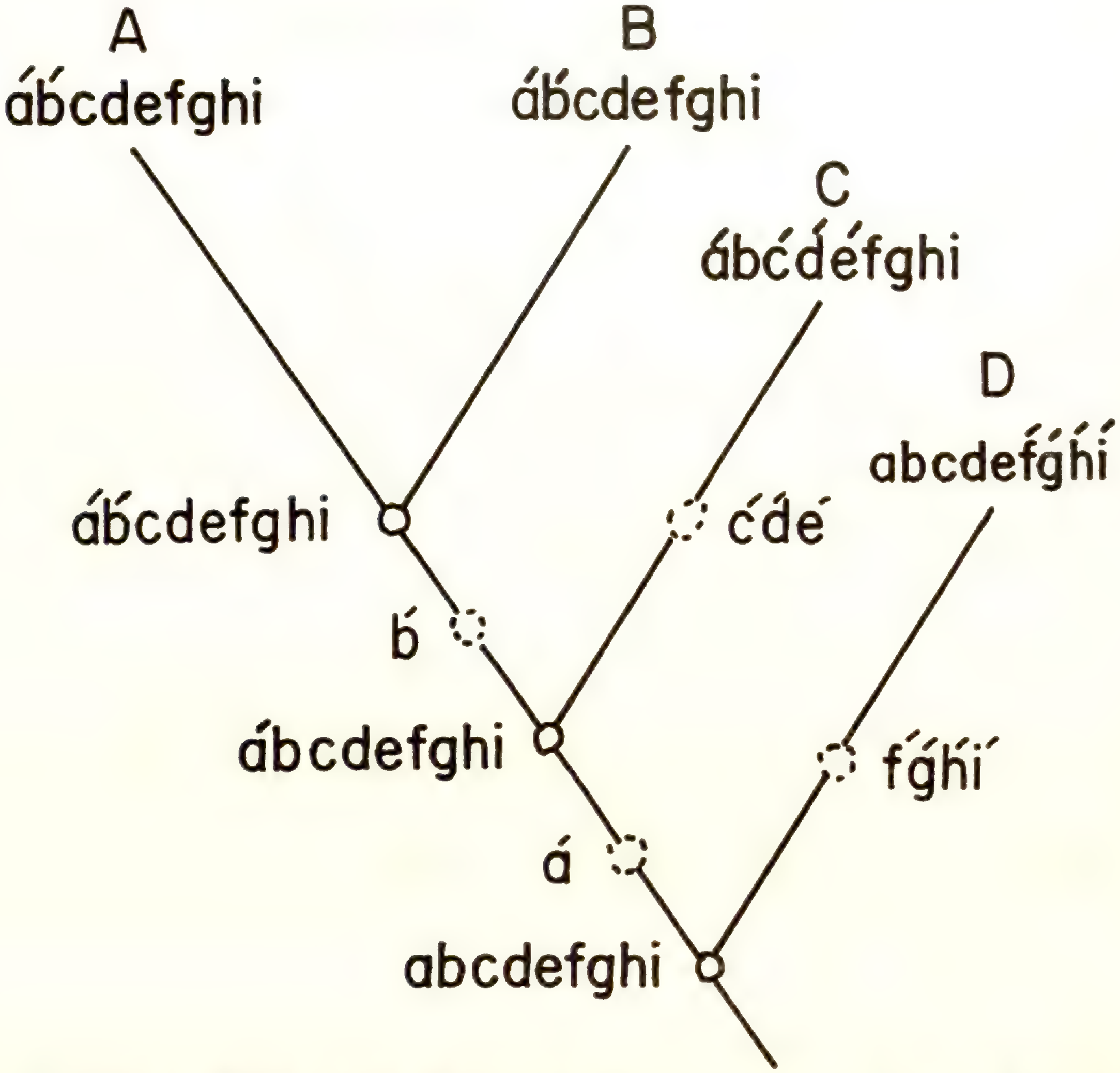

FIGURE 3. Diagram to show that phyletically more primitive groups (C,D) can possess a greater proportion of advanced character-states (letters with prime marks) than do phyletically more advanced taxa (A,B), which can have a greater proportion of primitive character-states (letters without prime marks). See text.

the phyletic sense (*contra* Nelson, 1972), although other phylogenetic systematists have made clear that centers of origin will reflect the distribution of genealogically primitive groups (Nelson, 1969, 1972; Cracraft, 1973*a*, 1973*b*, 1974*b*). Even this latter concept of primitive is sometimes ambiguous in that precise comparative statements are probably not possible in all cases. However, most workers have a general idea of what this means, and it is outside the content of this paper to pursue the idea in greater detail. Because hypotheses about the distributions of ancestral species are based on given concepts of phylogenetic relationships, the location of the center of origin will necessarily reflect the distribution of the phyletically primitive species. Unfortunately, we have very poor knowledge of relationships for most groups of organisms, and thus we seldom can make the precise biogeographic inferences that are possible when a particular phylogeny is well documented. Even though taxa that branched off earliest need not exhibit

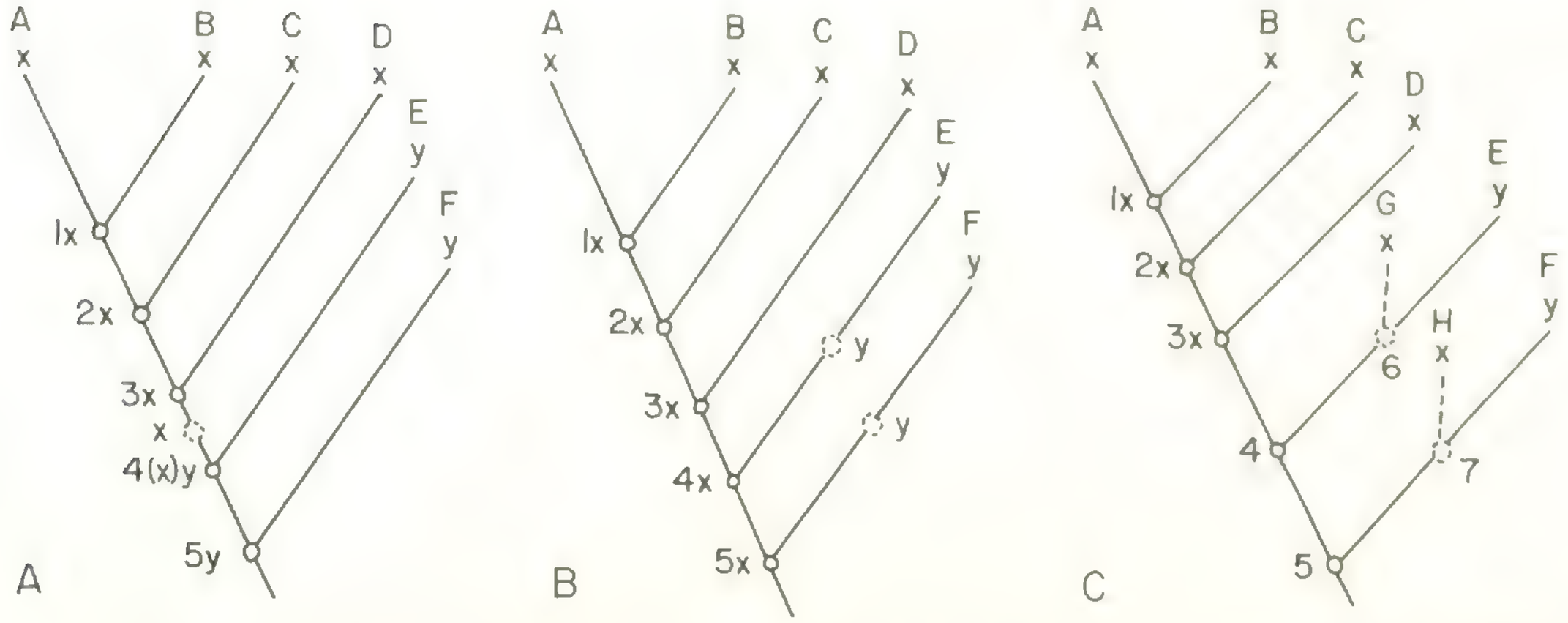

FIGURE 4. Three hypotheses for six taxa (A–F) found in two areas (x,y). In A hypotheses about the location of ancestral species (open circles, 1–5) are constructed using the reasoning of Hennig and Brundin; the center of origin of the group as a whole is postulated to be in y with one dispersal (dotted circle) to x. In B the hypothesis of Darlington is examined in that the center of origin is identified as the area (x) where advanced, dominant, highly diverse groups (assumed here to be taxa A–D) are found; it is thus necessary to postulate the independent dispersal of E and F to y. Hypothesis A is more parsimonious than B. In C the necessary conditions to fulfill the Darlington hypothesis (B) are examined; the presence of additional taxa (G,H) distributed in area x lend support to B. See text for additional details.

the greatest proportion of primitive characters (Fig. 3), it may be that they are, more often than not, more primitive morphologically than later groups. I believe this is the intuitive conclusion of most systematists and that it can be shown to be true for a number of groups.

Darlington (1957: 552–556), in contrast to advocates of the phylogenetic systematic approach, believes that primitive taxa are usually not located at the center of origin of a group but rather in more peripheral areas (see also Briggs, 1966, 1974; Horton, 1973). The resolution of the conflict lies in the way one presents a logically convincing argument that primitive groups are in peripheral areas in any specific instance. To my knowledge no classical evolutionary biogeographer presented these arguments, apparently because of a failure to realize, as Brundin (1972*a*: 74) notes, that "a careful establishment of strict monophyly and sister-group relationships is a necessary prerequisite for a realistic interpretation of a distribution pattern." Let us consider a distribution pattern of a monophyletic group (Fig. 4) in which four taxa (A–D) are located in area x and two other taxa (E–F), which are also the most primitive phyletically, in area y. Given the phylogeny depicted in Fig. 4, what biogeographic hypotheses can be constructed and which one is most parsimonious? In Fig. 4A the distribution of ancestral species (open circles) is determined using the reasoning advocated earlier. Perhaps the most parsimonious hypothesis is that species 4, which is ancestral to taxon E and its sister-group, A + B + C + D, was distributed in area xy, but because taxon F is distributed in area y, we might conclude that ancestral species 4 was probably also in y. If true, then sometime prior to the splitting of ancestral species 3 we would postulate dispersal (dotted circle) to area x. In Darlington's conception of this distribution pattern (Fig. 4B), where area x is considered the center of origin and primitive species are located peripherally in

area y, it would be necessary to postulate two independent dispersals to area y by the ancestors of E and F. The hypothesis of Fig. 4B is less parsimonious than that of Fig. 4A because it requires a greater number of dispersals to account for the distribution pattern. *This is not to argue the truth of either hypothesis, only their parsimony.*

But what conditions are necessary in order to satisfy the hypothesis of Darlington that primitive groups are distributed peripherally? Clearly we need additional taxa, fossil or Recent, related to taxa E and/or F and distributed in area x (I have omitted the possibility of other taxa, also in area x, that originated prior to ancestral species 4 or prior to species 5; in any case the reasoning is still similar). If we only had taxon G related to E as shown in Fig. 4C, then it would probably be most parsimonious to postulate that ancestral species 4 and 6 were distributed in xy (a clear choice between x and y cannot be made). If we only had taxon H related to F, then again it would be most parsimonious to postulate ancestral species 4, 5, and 7 to be in xy, but intuitively we would greatly suspect multiple invasions of area y. If both taxa G and H were known, an hypothesis of multiple invasions would probably be most parsimonious. In any case, the critics of the phylogenetic systematic theory of biogeography have not presented arguments of this kind, and therefore their claims for the peripheral distribution of primitive groups appear unsupported. There may be isolated examples of peripherally located primitive taxa, but I am unaware of any evidence, rigorously analyzed, that would suggest this to be a wide-spread phenomenon of animal distribution patterns.

The Problem of Fossils.—Phylogenetic systematists advocate a theory of historical biogeography that treats fossils much like Recent organisms; fossils are assumed to provide us with a point in space and time just as Recent organisms and are not assumed to possess any inherently special significance for constructing phylogenetic hypotheses (see Schaeffer *et al.*, 1972). Classical evolutionary biogeographers, on the contrary, often find fossils of special importance, thus Darlington's (1957: 35) remark that the "best clues [for biogeography], of course, are fossils—the right fossils in the right places. . . ." He goes on to note that fossils need to be interpreted carefully, but his biogeography relies heavily upon them nevertheless, and one is never given a clear exposition as to how they are to be interpreted.

It should be evident from the preceding discussions that the rules of inference used in phylogenetic systematic biogeography are applicable to either Recent or fossil taxa or both simultaneously. Indeed, it is not at all evident why fossils should be subject to a separate process of phylogenetic or biogeographic reasoning. If they can be, this has not yet been formalized. Set within a framework of a phylogenetic hypothesis, fossils can be extremely important for biogeographers, but considered outside this framework, the well known problems of recovery in space and time could easily result in erroneous interpretations.

APPROACH NO. 3: THE VICARIANCE MODEL

The two approaches to biogeography discussed above generally are concerned with recognizing centers of origin and pathways of dispersal; the geographical

history of the world's biota is considered interpretable within this framework. Yet another approach has been proposed which does not attempt to recognize centers of origin or dispersal pathways. The basic premises of this latter biogeographic model are (see Croizat, 1962; Croizat *et al.*, 1974):

1. The distribution of a group can be represented by one or more lines (tracks) connecting the ranges of all members of that group (subspecies of a species, species of a genus, etc.).

2. Many overlapping individual tracks between two areas form a generalized track which represents the distribution of an ancestral biota that has subsequently subdivided (vicariated) into the two descendant biotas.

3. Biotic distribution is to be looked upon as the result of subdivision (vicariance) of ancestral biotas rather than as origin in one region and dispersal to another.

4. Evidence for dispersal is seen in the sympatry of individual or generalized tracks.

The above four points briefly outline the approach advocated by Croizat (1952, 1958, 1962; see also Nelson, 1973, for a review of Croizat's work; DuRietz, 1940, applied the vicariance model to explain bipolar plant distributions). In his voluminous writings Croizat has never elucidated this model in a concise manner, but the main ideas of the vicariance of biotas can be found in *Space, Time, Form: The Biological Synthesis* (Croizat, 1962: 186–189, 209–210). The most detailed explication of the model, and the basis for much of the following comments, can be found in the paper by Croizat *et al.* (1974). Their position is best summarized by the following (Croizat *et al.*, 1974: 269):

"We conclude, therefore, that historical biogeography, *i.e.*, the study of the history of the world biota, is to be understood first in terms of the general patterns of vicariance displayed by the world biota. Sympatry (dispersal) means, after all, that a population has broken away from the original geographic constraints responsible for vicariance, and that the original vicariant pattern has, to some extent, become obscured as a result. Operationally, we consider that biogeographical investigation begins with the determination of general patterns of vicariance, and the determination of the geological changes that caused them."

Significance of the Vicariance Model.—Many of the principles embodied in the vicariance model have the potential for improving the study of biogeography. The model de-emphasizes the excessive reliance upon centers of origin and dispersal routes that has characterized biogeography since the time of Darwin (see, for example, Darlington, 1957; Ross, 1974: 209–244). Detailed discussions of chance dispersal that have little relevance for the discovery of important generalizations permeate the biogeographic literature. Most of this is rightly rejected by the vicariance model. Numerous studies, especially recent ones that attempt reinterpretations of "stabilist" biogeographic patterns in terms of the newer data on continental drift, have been based on prior conceptions about world geography and not on the patterns exhibited by the organisms themselves. This was one of the problems that forced Darlington (1957) to postulate numerous Holarctic dispersals and widespread extinctions to explain vertebrate distribution in the Southern Hemisphere. The vicariance model places primary emphasis on con-

structing hypotheses using biological data and not preconceptions about geological history and it is to Croizat's credit that he was one of the earliest biogeographers to insist that plant and animal distributions are not compatible with stable continents. Thus, the concept of generalized tracks focuses attention on the search for climatic and/or geographic factors that might have been responsible for the vicariance of ancestral biotas.

The vicariance model is applicable to the study of whole biotas instead of isolated groups, and in so doing forces upon the biogeographer a higher level of generality than is seen in most biogeographic analyses. The model stresses that biotas evolve as wholes and that significant changes in climate and/or geography must affect entire biotas. This viewpoint is too often ignored in traditional considerations of regional biogeography.

Finally, and perhaps most importantly, the model has significant explanatory powers with regard to the distribution of the world's flora and fauna. One of the best examples is the biota of the southern continents which, for the most part, can be interpreted satisfactorily in terms of an ancestral biota that was present at one time on the Gondwanaland supercontinent and is now fragmented (vicariated) due to continental breakup and drift (see following section). It is probably not necessary to interpret most of this biota in terms of centers of origin and dispersal and to do so involves the acceptance of unnecessary (nonparsimonious) assumptions. It is probable that by applying the vicariance model to the world's biota we will greatly increase our understanding of historical biogeography.

Criticisms of the Vicariance Model.—The vicariance model has been applied by relatively few workers (see Croizat *et al.* 1974, for a review), and no one other than Croizat (1952, 1958, 1962) has used it to interpret a large segment of the world's biota. The following comments are designed to focus attention on what seem to be the major problems with the model as it is currently stated and with the ways certain biogeographic data can be interpreted using the model.

The precise relationship between phylogeny and biogeography has not been fully discussed by advocates of the vicariance model. Whereas Croizat (1952: 526) does appear to acknowledge a close connection between phylogeny and biogeography, he has not defined this connection in any precise manner and occasionally suggests that biogeography is not "subordinate" or "subservient" to "taxonomy" (Croizat, 1952: 546, 1970: 317). Most of Croizat's systematic data come from studies having a strong bias toward evolutionary systematics and most of these workers were interested in questions of classification and not phylogeny (I base this conclusion on an examination of Croizat's extensive ornithological examples and those from other vertebrates with which I am familiar). Hence, I cannot agree with Nelson (1973: 315) that Croizat's biogeography is very similar to the biogeography of phylogenetic systematists, at least certainly not in the theoretical foundations of each system (*e.g.*, Nelson, 1973: 316). I believe, on the other hand, that the two approaches can be made more or less compatible as Croizat *et al.* (1974) have attempted to do (see comments below).

Croizat's basic datum is the "track" which he considers to be "factual," although he recognizes this interpretation can be questioned (Croizat, 1962: 7–8). My interpretation is that "tracks" are highly theoretical constructs in that some concept

(typically, of relationships) forms the basis of interposing a track between two areas. More attention should be paid to exactly how tracks are to be drawn. If tracks are to represent connections between "sister-groups," then indeed Croizatian biogeography may have something in common with that of the phylogenetic systematists. However, to my knowledge Croizat himself has never specified that tracks are to have this rather precise meaning, and it is reasonably clear from his examples that tracks frequently do not represent sister-group relationships. Indeed, this is not unexpected, because of his reliance on the work of evolutionary systematists whose concept of relationship is not equivalent to that of phylogenetic systematists.[4]

A major problem facing biogeographic analysis is the manner in which dispersal is to be treated as part of a biogeographic hypothesis. I agree with Croizat *et al.* (1974) that when analyzing the history of biotas we must first attempt to understand the general patterns of vicariance, and then, following this, consider whether it is necessary to invoke dispersal to explain the composition of the biota. Nevertheless, an important issue is deciding under what circumstances we can claim that vicariance has explained a particular biogeographic pattern. The vicariance model assumes that a generalized track between two areas is *prima facie* evidence for an ancestral biota that has subdivided (Croizat *et al.*, 1974). In my opinion vicariance of an ancestral biota should only be claimed when one can also identify the event causing vicariance; without this, vicariance as an explanation for historical change is incomplete. This requirement appears consonant with Croizat's panbiogeographic method—that is, the physical and biotic environments evolve together and biogeography is directed toward understanding that unity (Croizat, 1962). In most cases a generalized track probably represents a subdivided ancestral biota, but the generality of this assumption needs to be established more firmly. Thus, we should discover what percentage of generalized tracks can be explained by vicariance and what percentage cannot. We might expect that the largest, most thoroughly documented, generalized tracks will be correlated with easily recognized vicariant events. But is a generalized track in itself sufficient evidence for hypothesizing an ancestral biota that has been subdivided? Perhaps not. It is questionable whether vicariance should be invoked if there is substantial geological evidence against a vicariant event. The most likely examples of this situation involve the biotas of oceanic islands. Either we assume that an as yet unknown vicariant event was responsible for the generalized track to the mainland, despite current geological thinking against such an event, or we accept current geology and invoke dispersal. The importance of geological evidence in constructing biogeographic hypotheses using the vicariance model seems clear. Thus, one cannot use the generalized track connecting the land biotas

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[4] This is not a criticism of panbiogeography *per se*, because clearly Croizat has had to use the available literature. However, it does seem relevant to the arguments of those who wish to draw an unduly close parallel between the biogeography of Croizat and that of phylogenetic systematists. If one is dealing with a large number of tracks between two areas, *e.g.*, Africa and South America, then knowledge of a precise sister-group relationship of each link may not be necessary. We still would be compelled to explain this disjunct distribution. On the other hand, where there are few links, as in New Zealand and South American vertebrates, knowledge that these similarities are sister-group relationships strengthens the argument for vicariance.

of South and Central America as evidence against watergaps preventing dispersal between the two areas (Croizat, 1958, personal communication), while at the same time using the generalized track between the marine biotas of the Caribbean and Pacific as evidence for a vicariant event (closure of the Panamanian landbridge) that subdivided the ancestral marine biota (Croizat *et al.*, 1974).

A final problem needing further discussion is the extent to which biogeographers will seek to explain the vicariance of all taxa of a particular generalized track as the result of the same climatic and/or geographic event. As an example, one could make a strong argument against interpreting all sister-group relationships between South America and Africa as the result of the vicariance of an ancestral biota when the two continents separated about 90 million years ago. Despite the problems of judgment involved in many cases, biogeographers can take information from the fossil record and from a knowledge of relationships and use this to compare probable times of branching with various climatic and/or geologic events. In this way it may be possible to avoid interpretations such as those of Croizat (1970) in which the history of certain avian species and subspecies is thought of as the result of vicariance in the Mesozoic.

DISTRIBUTIONAL PATTERNS: EXAMINATION OF BIOGEOGRAPHIC MODELS

It will be the purpose of this section to suggest that a number of intercontinental distribution patterns for both plants and animals are best explained by the vicariance of ancestral biotas at the time of continental breakup whereas other patterns can be explained best by the dispersal of one biota into another. Thus, we will be examining the power of the previously discussed biogeographic models to explain generalized distribution patterns among continents. I will attempt to show that most of these patterns are relatively consistent with our present knowledge of intercontinental paleogeography and that the extent to which a particular biogeographic model can explain the biologic data is also dependent to a large extent upon the presumed paleogeography.

Throughout this discussion I only propose to treat what appear to be major biogeographic patterns among the larger continents; many smaller, secondary patterns wil be ignored. I will first define these patterns for vertebrates (see review in Cracraft, 1974*b*, 1975) and then attempt to generalize them for plants, and where possible, for invertebrates, trying to point out the concordance or discordance of these biologic data. Naturally, because of the paucity of phylogenetic information for many groups of organisms, the generality of the patterns can only be tentatively postulated in some cases.

PRINCIPAL VICARIANT PATTERNS

South America-Africa.—The vertebrate faunal links between close relatives are stronger between South America and Africa than for any two other southern continents (Cracraft, 1974*b*, 1975). Nearly all of these trans-Atlantic associations involve taxa that are predominately tropical. They include at least seven groups of fresh-water fishes, five of amphibians, four of reptiles, two of birds, but no mammals (Table 1). The list of Table 1 comprises those taxa that were most probably representative of or derived from the ancestral biota present on the

TABLE 1. Vertebrate links (sister-groups) between South America and Africa. See Cracraft (1973*b*, 1974*b*, 1975) for details.

South America	Africa
Fresh-water fishes	
Lepidosirenidae	Lepidosirenidae
Osteoglossidae	Osteoglossidae
Characidae	Characidae
Siluriformes	Siluriformes
Nandidae	Nandidae
Cichlidae	Cichlidae
Cyprinodontidae	Cyprinodontidae
Amphibians	
Pipidae	Pipidae
Leptodactylidae	Leptodactylidae
Bufonidae	Bufonidae
Microhylidae	Microhylidae
Caeciliidae	Caeciliidae
Reptiles	
Iguanidae	Agamidae
Gekkonidae	Gekkonidae
Teiidae	Lacertidae
Boinae	Pythoninae
Birds	
Rheinae	Struthioninae
Other suboscines	Eurylaimidae, Pittidae, Philepittidae

combined continent prior to final breakup in the early Late Cretaceous. If one included the fairly substantial number of taxa that probably dispersed across the Cretaceous-Tertiary watergap, the list for birds would be increased rather markedly and that for mammals would be expanded to include caviomorph rodents and monkeys.

It is to be expected that the links between South America and Africa are strongest in the presumably older groups of vertebrates and that they involve the tropical element of these faunas. The area of Brazil-Gabon was the site of final separation, and presumably this region has been tropical throughout the last 200 million years.

What is the nature of the pattern in other organisms? The rather marked similarities in the floras of South America and Africa have been discussed by Axelrod (1970), Raven & Axelrod (1974), Thorne (1972, 1973), and Smith (1973). However, the interpretations placed on these similarities differ among these authors, Axelrod and Raven favoring an explanation greatly dependent upon the Mesozoic continuity of the floras, Thorne and Smith preferring long-distance dispersal after continental breakup. Thus, Thorne (1973: 45) believes that the botanical evidence "argues against continental drift as a significant factor in explaining the distribution of seed plants between Africa and South America. If

continental displacement has occurred, the separation of Africa and South America must have attained its present state, or largely so, before the development of the present seed-plant floras of the world, certainly previous to Tertiary and Late Cretaceous time and possibly even previous to Jurassic time."

Data presented by many botanists, some of whom are cited above, strongly indicates that distribution patterns of plants between South America and Africa and among the other southern continents (see below) are basically similar to those of vertebrates and consequently are consistent with the hypothesis of a fragmented Mesozoic biota. Most importantly, I want to suggest that the point of controversy should not be whether continental drift is or is not the explanation for the similarities of the two floras but rather which biogeographic model—vicariant or dispersal—best explains the distributional data.

The similarities of the African and South American floras are impressive. About 276 families are present in the combined flora and 186 are shared; both continents have between 40 and 50 families not shared with the other (Thorne, 1972, 1973). The number of links between these two continents might be further increased if possible sister-group relationships among families could be identified. As far as I am aware, this aspect of plant phylogenetics has played little role in the debates about Southern Hemisphere biogeography or in botany in general (see below, PHYLOGENETIC ANALYSIS OF *NOTHOFAGUS* BIOGEOGRAPHY). Thus, how many of the 40 to 50 South American families not found in Africa have their closest relative on the latter continent? The same could be asked for the African taxa not found in South America. Can we ascribe the isolation of sister-groups on the two continents to divergence following continental breakup as we surely can among a number of vertebrate taxa (Cracraft, 1974*b*, 1975)? The argument that long-distance dispersal may occur in some or many taxa hardly invalidates the real issue which is the pervasive pattern of phylogenetic relationships among the floral elements of South America and Africa. It is probably futile to speculate on the number of long-distance dispersal events needed to account for the 186 or more links because (1) dispersal is best postulated in taxa that are not part of a well-defined generalized distribution pattern (see Croizat *et al.*, 1974), and (2) there is, in this case, a well documented vicariant event in the early Late Cretaceous separation of the two continents. *I am not arguing against the possibility of long-distance dispersal for any particular taxon, only against its relevance for explaining a major biogeographic pattern when a vicariant event is known.* If parsimony is to be the criterion for choosing among alternative biogeographic hypotheses, as it is in other sciences, then I believe we have to prefer the vicariant hypothesis in this case.

In order to strengthen the above interpretation and to lay groundwork for later discussions, I want to examine several of the arguments proposed by Thorne (1972, 1973) and Smith (1973) against the vicariant pattern of South American and African floras. The major arguments are:

(a) *About 48 African families and 42 South American families have failed to establish trans-Atlantic distributions; these numbers are considered too great if there was once a common flora.* These differences can hardly negate the trans-Atlantic patterns. As noted above, some of these endemics may have

sister-groups on the other continent and thus are themselves links. Some are undoubtedly related to plants in other areas, *e.g.*, to North America or Eurasia, or they may be the result of evolutionary origin and divergence subsequent to continental separation.

(b) *Only 12 families are restricted to South America and Africa.* This is not an important objection in light of the fact that the flora shared between Africa and South America is predominantly tropical and part of a circum-tropical flora of Pangaea. Hence, it is reasonable to expect many of the families to be shared with other tropical regions (see below).

(c) *There is a very strong amphi-Pacific distribution pattern among plants and this is inconsistent with trans-Atlantic vicariance.* The links between Africa and South America must still be explained. The amphi-Pacific similarities very probably reflect the Mesozoic circum-tropical distribution pattern prior to continental separation.

(d) *The Hawaiian Islands received their flora by long-distance dispersal so why not Africa and South America.* These are not comparable situations. In the former we have no evidence for a vicariant event between Hawaii and another land mass, in the trans-Atlantic example we do. It is simply a matter of applying the most economical hypothesis in each case.

The trans-Atlantic relationships of invertebrates are still poorly known. Keast (1972) has reviewed some of the links among Oligochaeta, onychophorans, pseudoscorpions, and many insect groups. It is impossible to tell right now how strong invertebrate links are until much more systematic work is completed.

In summary, distributional data for plants and vertebrates strongly point to the existence of a common ancestral biota on a joined South American-African continent (see especially Raven & Axelrod, 1974: 603–604). This ancestral biota was composed primarily of tropical elements. The similarities between Africa and South America are explained most parsimoniously by vicariance of this ancestral biota.

South America-Australia.—The probable sister-group relationships between South American and Australian vertebrates are shown in Table 2 (Cracraft, 1974*b*, 1975). The links between the two areas are fairly substantial, but they are not as strong as those for South America and Africa. A further important point is that a well-defined tropical component of this fauna is not readily apparent as it was for the South American-African biota. On the other hand, the biota is also not strongly cool-temperate in aspect. Many authors have commented on the similarities of the floras of South America and Australasia, but the plant links between these two areas are in need of more detailed analysis (see DuRietz, 1940, for an admirable review of the earlier literature). It seems probable that these similarities are of two types: (1) basically tropical taxa that are either pantropical or undoubtedly were in the past but are now extinct in Africa and/or southern Asia—in any case, Australian representatives of these groups have predominantly southern Asian affinities, and (2) those taxa, probably temperate or cool-temperate, having links across East Antarctica. A number of botanists, including both those workers supporting and those denying the importance of continental drift for plant distribution, have used (rather loosely sometimes) the

TABLE 2. Vertebrate links (sister-groups) between South America and Australia. See Cracraft (1973*b*, 1974*b*, 1975) for details.

South America	Australia
Fresh-water fishes	
Ceratodontidae	Ceratodontidae
Osteoglossidae	Osteoglossidae
Amphibians	
Hylidae	Hylidae
Leptodactylidae	Leptodactylidae
Reptiles	
Meiolanidae	Meiolanidae
Chelyidae	Chelyidae
Birds	
Struthionidae	Casuariidae
Suborder Galli	Megapodiidae
Mammals	
Metatheria	Metatheria

concept of an Australasian or Indo-Australasian flora without clearly distinguishing these two components, or possibly others.

Botanists have commented that the links of Australia and South America via East Antarctica are primarily of temperate or cool-temperate taxa (Good, 1964; Burbidge, 1960; Raven & Axelrod, 1972, 1974; Raven, 1972; Thorne, 1972). It is also evident that in terms of numbers, far fewer taxa link Australia and South America than link the tropical floras of the southern continents. Thus, the botanical evidence suggests probable temperate relationships of Australian taxa to South America and tropical links to the warm areas of the Old World. As Raven & Axelrod (1974) have suggested, these tropical patterns may have been initiated via Southeast Asia as the Australian plate moved northward in the Cenozoic or possibly via Africa-India-East Antarctica in the Cretaceous prior to major continental disruption.

The above patterns for plants are quite consistent with those for vertebrates. The links of both are less strong between South America and Australia than between the other continents, especially between Australia and the tropical regions of southeastern Asia (see below). Many invertebrates show these same distribution patterns, and some of them have been reviewed by Keast (1972). Diverse groups such as earthworms, spiders, fresh-water molluscs, fresh-water crayfishes, and many insects show relationships between South American and Australian taxa. Within the chironomid midges, for example, there are at least nine links among genera of the Podonominae and Aphroteniinae (Brundin, 1966).

The biological and geological evidence, therefore, seems very consistent with the existence of a Cretaceous-early Tertiary biota common to Australia, East Antarctica, and South America. Apparently this biota was predominantly

TABLE 3. Vertebrate links (sister-groups) between South America and New Zealand. See Cracraft (1974*b*, 1975) for details.

South America	New Zealand
Amphibians	
Leiopelmatidae	Leiopelmatidae
Birds	
All other ratites (infraorder Struthiones)	Dinornithidae, Apterygidae (infraorder Apteryges)
Spheniscidae	Spheniscidae

temperate, and its present disjunct nature is explainable in terms of vicariance of the ancestral biota.

South America-New Zealand.—The vertebrate patterns between South America and New Zealand are indeed weak, but the relationships of certain taxa are clearly trans-Antarctic and not trans-Tasman (Table 3). It is of interest that those vertebrate links that do exist between South America and New Zealand are clearly of the oldest taxa in the fauna; none of the presumably younger elements are represented.

The close floristic relationships of New Zealand and southern South America have been well documented (Godley, 1960; Couper, 1960; Raven & Axelrod, 1972; Good, 1964). Almost all of these links are within cool-temperate taxa. Invertebrates also exhibit relationships between these two continents (Keast, 1972). The best documented examples are within chironomid midges where Brundin (1966) has discovered at least six or seven links between these two areas.

The evidence, then, is consistent with the presence of an austral biota common to New Zealand, West Antarctica, and southern South America that was fragmented by continental breakup.

North America-Eurasia.—The similarities of the North American and Eurasian vertebrate fauna are well known, and it will not be my purpose here to recapitulate all these similarities (see Darlington, 1957). Elsewhere I categorized the Recent vertebrate families with respect to primary Gondwanaland or Laurasian Faunal Elements (Cracraft, 1974*b*). The latter element included 16 families of freshwater fishes, 13 of amphibians, and 17 of reptiles. Additionally, many families of birds including the bulk of the passerines (Mayr, 1946; Cracraft, 1973*a*) and placental mammals (McKenna, 1969; Simpson, 1947) can be classified as Laurasian in origin.

Similarly, the floral similarities between North America and Eurasia have long been recognized, and summaries can be found in Thorne (1972), Leopold & MacGinitie (1972), Wolfe (1972), and Wolfe & Leopold (1967).

All of these biotic relationships are best interpreted in terms of divergence following vicariance of more widespread ancestral faunas and floras. Obviously some of the vicariant events occurred at different times. An important one was the opening of the North Atlantic in the Eocene, and present evidence indicates that there have been repeated closures and openings of the Bering Straits during

the Tertiary. Thus, in most cases it is not necessary to invoke dispersal as an explanation for the general biotic similarities of North America and Eurasia.

Tropical Old World.—A final major ancestral biota that was fragmented is that of the Old World tropics. In an earlier paper (Cracraft, 1973*b*) the role of dispersal in accounting for similarities throughout this area was overemphasized, although dispersal from one region to another has undoubtedly occurred in some groups. Thus, many of the Recent disjunct patterns between tropical Africa and tropical Asia are best interpreted as vicariance of a once widespread biota. The situation is complicated in that there have been repeated vicariant events within the fauna by rising and lowering seas and in the Tertiary by orogenic and climatic changes brought about by the collision of India. However, at various times the ancestral biota has included a large number of vertebrate taxa: cypriniform, siluriform, perciform, channiform, and osteoglossiform fishes; caeciliid, bufonid, ranid, and microhylid amphibians; agamid, gekkonid, lacertid, scincid, boid, elapid, and viperid reptiles; and many taxa of birds and mammals (Cracraft, 1973*a*, 1973*b*, 1974*b*).

The similarities in the tropical flora of Africa and southern Asia have been amply documented by Axelrod (1970, 1972), Thorne (1972), and others. The distribution patterns exhibited by both plants and animals across the Old World tropics require a unifying explanation. The most reasonable hypothesis is that of a common biota that has become vicariated; most of the Recent patterns can be explained by disruption and retreat of tropical elements toward Africa and southeastern Asia as much of southern Asia became drier in the Neogene (Axelrod, 1974).

PATTERNS OF DISPERSAL AND MERGING FAUNAS

I now want to discuss two examples of intercontinental biotas in which the links (tracks) are best explained by dispersal of one biota into another rather than by vicariance.

South America-North America.—The geological evidence points very strongly to rather substantial separation of South and North America during the late Jurassic and Cretaceous (see review of evidence in Cracraft, 1974*b*; Raven & Axelrod, 1974). Then, in the Tertiary, southern Central America was gradually built up, increasing the proximity of the two areas until final connection in the Plio-Pleistocene.

Without arguing the details about precisely when a specific group may or may not have dispersed from one area to the other, evidence based on phylogenetic and speciation patterns, levels of differentiation, and diversity gradients strongly suggests that there has been significant interchange of the biotas of North and South America, primarily during the Tertiary although some probably occurred earlier. Among vertebrates, those taxa of the Gondwanaland Faunal Element that dispersed northward included cichlid, characid, and siluriform fishes; microhylid, hylid, bufonid, and leptodactylid amphibians; iguanid and teiid reptiles; suboscine birds; and marsupial mammals. Those North American (Laurasian) taxa dispersing southward into South America probably included ranid frogs, salamanders, possibly scincid and colubrid reptiles, passerine birds, and placental mammals.

Evidence of a merging of biotas is also seen in plants (Thorne, 1972; Raven & Axelrod, 1974). South America seems to have contributed tropical elements to North America, whereas the latter contributed mainly temperate elements to South America.

Some of the similarities of the North and South American biota may be the result of vicariance of the Pangaean biota (*e.g.*, among primitive fishes and frogs). If true, these links must represent only the most ancient taxa. Present information indicates that the similarities were initiated long after the breakup of Pangaea.

Australia-Southeast Asia.—The close relationship between many Australian taxa and groups in southern Asia suggests that a common explanation should be sought for this well-defined pattern. In this case, the main pattern is not explicable by vicariance of an ancestral biota (except on a localized scale; see below) but rather by the merging of two faunal elements.

Many Australian vertebrates are more closely related to taxa in Asia than to those in South America. These include ranid, possibly microhylid frogs; agamid, scincid, varanid, pythonine, colubrid, and elapid reptiles; essentially all the oscine passerine birds and many nonpasseriforms as well; and murid rodents. Likewise, a diverse assemblage of plants show distribution patterns similar to those of vertebrates (Axelrod, 1970, 1972; Thorne, 1972; Raven & Axelrod, 1972).

The links between Australia-New Guinea and the Asian continental block are best interpreted as dispersal of one fauna into another at the time the two plates were approaching or after collision. On the other hand, the similarities one sees within any one plate, for example, among the islands of the Asian continental shelf, can be explained by vicariance of a widespread biota present when sea levels were much lower. The same explanation readily applies to the vicariant pattern one sees in the plants and animals of Australia and New Guinea.

Phylogenetic Analysis of *Nothofagus* Biogeography

The southern beeches, *Nothofagus*, are a well known and often cited example of a biogeographically important plant genus. Despite a number of discussions (Godley, 1960; Darlington, 1965; Brundin, 1966; Melville, 1966; Keast, 1972; Moore, 1972; van Steenis, 1972), the biogeography of *Nothofagus* is not known in any detail, most authors merely pointing out that the different "species-groups" are each widely distributed on southern continents. It is known that the dispersal capabilities of *Nothofagus* are greatly restricted (Preest, 1963), thus most authors have concluded that continuous land connections were probably necessary to produce its distributional pattern. Darlington (1965), on the other hand, argued for multiple, independent derivation of *Nothofagus* from the Northern Hemisphere.

In all these writings little mention has been made of the role that phylogenetic relationships might play in deciphering *Nothofagus* biogeography. To my knowledge only Brundin (1966) has discussed this subject with any insight. He noted that because phylogenetic relationships are essentially unknown, it is not possible to reconstruct the exact nature of the distributional patterns within the genus. Brundin's comments on *Nothofagus* have wide applicability for plant

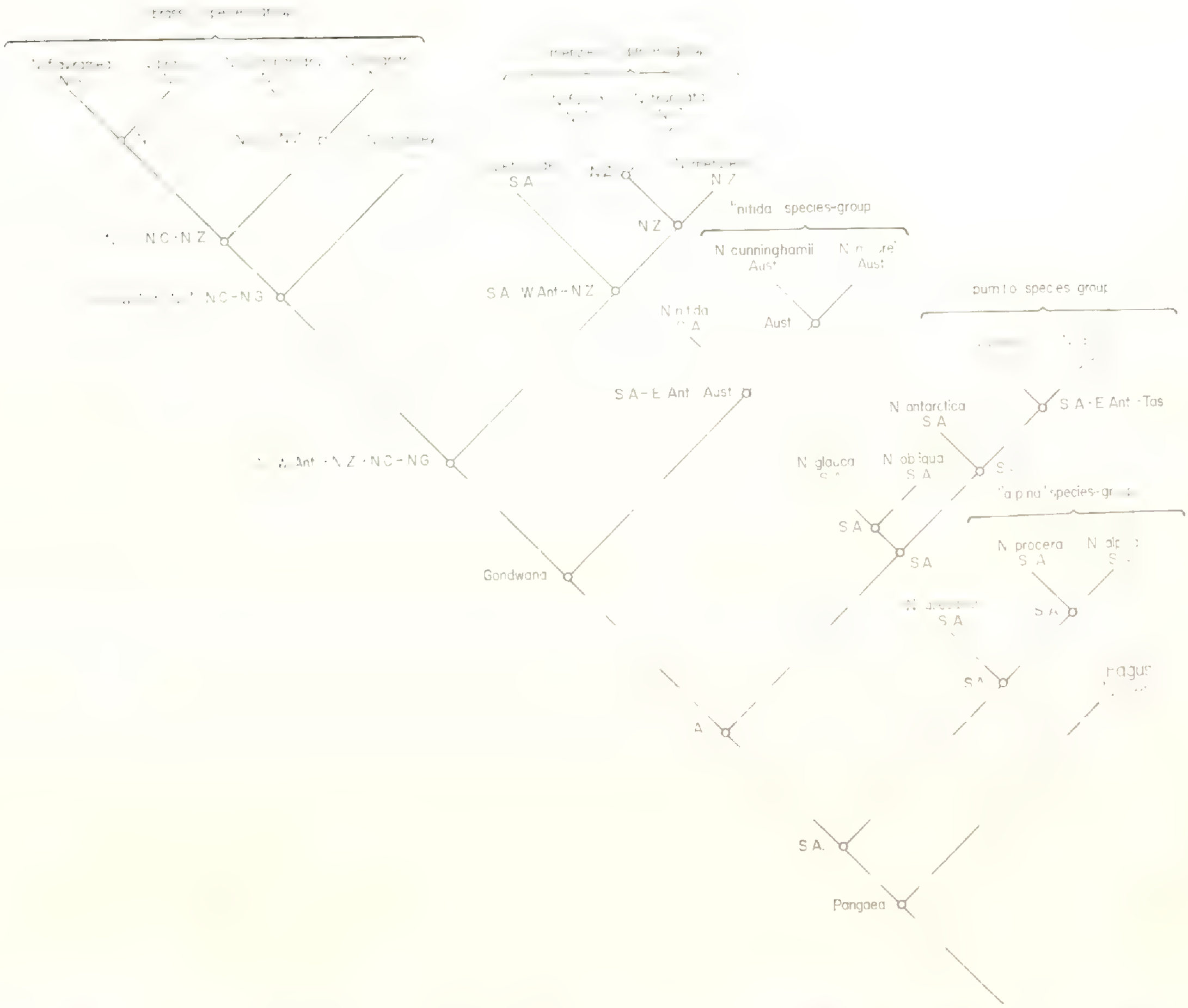

FIGURE 5. A phylogeny of the species of *Nothofagus* (based on Melville, 1973) and a biogeography deduced from it (see text for details). Geographical distributions of hypothetical ancestral species (open circles) are hypothesized. Note that "species-group" names are used for descriptive purposes only and do not refer to traditional groupings based on pollen morphology.

biogeography, for the vast majority of workers in this field have not appreciated the importance of a phylogenetic systematic approach to biogeography.

Recently, Melville (1973) proposed a phylogeny of *Nothofagus* species. His treatment of the biogeographic implications of these relationships was brief. In the discussion that follows I want to use his phylogeny as a basis for reconstructing the biogeographic history of *Nothofagus*. This is considered important because (1) it will be the first attempt at a detailed reconstruction of *Nothofagus* based on a given phylogeny, and (2) it serves as a demonstration of the importance and applicability of phylogenetic systematics to plant biogeography. I emphasize that I am using Melville's phylogeny to illustrate a theoretical point. I am fully aware that fossil data have not been interpolated into the phylogeny. In the case of *Nothofagus* the fossil record must be viewed with a grain of scepticism: it is based almost entirely on pollen morphology, which may not provide sufficient phylogenetic information to allow meaningful biogeographic deductions (see below).

The following biogeographic interpretations are deduced from the phylogeny shown in Fig. 5. It is not my purpose to debate the validity of the phylogeny (Melville provided little supporting evidence), but rather to use it as an example of the reasoning that has been applied extensively to animal distribution (Hennig, 1966*a*; Brundin, 1966; Nelson, 1969; Cracraft, 1973*a*). In Fig. 5 I have postulated the geographical distribution of the hypothetical ancestors (open circles) of the different lineages.

The biogeography of *Nothofagus* is organized around four separate trans-Antarctic relationships. The first ("*brassii*" species-group[5]) involves *N. dombeyi* of South America and its sister-group of four species in New Guinea, New Caledonia, and New Zealand; the second ("*menziesii*" species-group) is between *N. betuloides* of South America and its sister-group of three species in New Zealand; the third ("*nitida*" species-group) is *N. nitida* of South America and its sister-group of two species in Australia; and the fourth ("*pumilio*" species-group) is *N. pumilio* of South America and its sister-species, *N. gunnii*, of Tasmania. Two of these links involve relationships across East Antarctica and two across West Antarctica.

One can visualize that the common ancestor of the "*brassii*" species-group was distributed throughout a land mass comprising South America, West Antarctica, New Zealand, New Caledonia, and New Guinea. Separation of the New Zealand continental block away from West Antarctica and South America vicariated the ancestral species into *N. dombeyi* and its sister-group. Later, vicariance isolated the ancestor of *N. flaviramea* and *N. brassii* in New Guinea and the ancestor of *N. codonandra* and *N. solandri* on a land mass including New Zealand and New Caledonia. A subsequent vicariant event, possibly subsidence of the intervening continental crust, isolated *N. codonandra* in New Caledonia and *N. solandri* in New Zealand. All of the above vicariant events, their geography and sequence, are reasonably consistent with what we know of the geology of the region (Raven & Axelrod, 1972).

The common ancestor of the "*menziesii*" species-group was likewise distributed over South America, West Antarctica, and New Zealand prior to continental breakup. When continental separation finally occurred, *N. betuloides* was isolated in South America and the ancestor of *N. fusca*, *N. truncata*, and *N. menziesii* was isolated in New Zealand. Regional geographic isolation within New Zealand can account for the speciation of the three species there.

The ancestor of the "*nitida*" species-group was apparently distributed in South America, East Antarctica, and Australia. Continental fragmentation can be postulated to have isolated *N. nitida* in South America and *N. cunninghamii* and *N. moorei* in Australia.

Within the "*pumilio*" species-group the ancestor of *N. pumilio* and *N. gunnii* is postulated as being distributed in South America, East Antarctica, and Tasmania. Continental fragmentation thus isolated *N. pumilio* in South America and *N. gunnii* in Tasmania. Because of the distribution of *N. antarctica*, *N. glauca*, and

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[5] Species-group names are applied here merely for convenience of discussion and no taxonomic significance is necessarily implied.

N. obliqua in South America, the ancestor of the entire "*pumilio*" species-group was probably South American.

Finally, the "*alpina*" species-group probably has had its entire history in South America. Localized geographic isolation can account for speciation there.

Several important points can be made about the biogeography just postulated. It must be emphasized, however, that the above biogeographic hypothesis is based only on the phylogeny of Fig. 5 and has been presented more as an example of reasoning that might be used in biogeography rather than as a distributional history of *Nothofagus* itself. First, given the hypothesis of Fig. 5, the genus *Nothofagus* provides four trans-Antarctic links, not just one. It may be supposed that a phylogenetic analysis of other plant genera (and families) might also provide evidence of multiple links.

Second, using the hypothesis, it is not necessary to advocate wholesale long-distance dispersal to account for the distribution of the genus around the southern end of the world. Some dispersal may have occurred at various stages in the phylogeny. For example, one might deduce from the phyletic data that the early history of the genus was primarily South American and that subsequent to the origin of the "*pumilio*" species-group there was dispersal to other areas of Gondwanaland. Likewise, the "*menziesii*" and "*brassii*" species-groups probably attained an independent distribution across West Antarctica. Since it is unlikely that a vicariant event occurred across the entire area of South America, West Antarctica, and New Zealand, some dispersal is suggested. Nevertheless, it must be stressed that within the phylogeny of the genus as a whole, dispersal need not be accepted as the prime cause for the Recent distribution pattern.

Third, if the distributional history of *Nothofagus* outlined here is close to reality then it is remarkably consistent with the patterns of vertebrates and invertebrates. This also suggests a common biogeographic history for Southern Hemisphere biota. Patterns for *Nothofagus* show a track from South America across West Antarctica to New Zealand and across East Antarctica to Australia or Tasmania. There are no sister-group relationships between species in Australia and those in New Zealand. Interestingly, there are no close relationships of species in Australia and New Guinea, the latter area showing relationships to New Caledonia and New Zealand. This latter distribution is consistent with past geology, since these areas may have been more or less contiguous before opening of the northern part of the Tasman Sea. Other plant groups show tracks from New Guinea through New Caledonia to New Zealand (Croizat, 1952; Burbidge, 1960).

It is obvious from his phylogeny that Melville (1973) does not consider the traditional "species-groups" which are based on pollen morphology (the *menziesii*, *brassii*, and *fusca* species-groups of most authors; not those of Fig. 5) to be natural groups. Indeed, I am unaware of any evidence that strongly suggests that the three different pollen types characterize monophyletic taxa. Such evidence could only come from a detailed analysis in which ancestral-derived polarities in pollen morphologies could be hypothesized. In this way supposed monophyletic taxa will not be erected on the basis of shared primitive character-states but rather on shared advanced character-states (Hennig, 1966*b*; Brundin, 1966). This uncertainty about relationships within *Nothofagus* casts great doubts on the systematic

allocation of fossil pollen and any biogeographic interpretations one might draw from them. Biologists have blithely assumed that pollen morphology defines related species-groups, but that may very well not be the case within some, but not necessarily all, species-groups. Relationships within *Nothofagus* are in need of restudy before the biogeographic conclusions of previous authors can be accepted or rejected.

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PHYLOGENETIC BIOGEOGRAPHY OF MAYFLIES[1]

GEORGE F. EDMUNDS, JR.[2]

The number of biogeographers who confidently drew dispersal routes on fixed continent maps ten or more years ago and now just as confidently draw dispersals of the same organisms on continental drift maps must cause us to seriously question the procedures of biogeographers. Because of its complexity, biogeography is unlikely to easily make the transition to a precise science, but certainly it is possible to greatly increase the rigor of the basic principles and procedures and avoid intuitive assessments of distribution patterns within the constraints of preconceived notions. I would like to discuss the approach to biogeography that I find most useful, and to express objections to some of the practices and viewpoints common among biogeographers.

I have spent most of my academic career running against the current of prevalent biogeographic opinion and many continue to believe that my phylogenetic methods are not valid, but my results generally conform to the patterns of earth history from plate tectonics. I was trained in Neo-Matthewian biogeography, but as a mayfly worker I have not been seriously influenced by such dogma. Every worker treating the mayflies of Chile and adjacent Argentina has recognized the relationship of these mayflies to those of Australia and New Zealand. Furthermore, I was strongly influenced by C. P. Alexander of the University of Massachusetts who in numerous papers on craneflies has clearly recognized these austral affinities. For example, in 1929, he noted that the close affinities of the craneflies from Chile-Patagonia, New Zealand and Australia gave evidence "overwhelmingly in favor" of a former Antarctic land connection to explain the distribution pattern (Alexander, 1929). Early in my career I was told by a famed vertebrate zoologist that the evidence that I had of closely related mayflies in Chile, New Zealand and Australia meant little because insect studies had not reached a significant level of sophistication, and even if I was correct, the distribution of these insects could be explained by island hopping. This event increased my determination to do first hand detailed studies on these austral disjuncts.

The fixed continent dogma led many investigators who found, for example, related organisms only in southern Chile-Argentina and southeast Australia to explain such distribution through tortuous rationalizations. Some drew a dispersal arrow through Asia, the Bering Sea, and North and South America. Others decided that the organisms were obviously cases of parallel evolution. Still others invoked long distance dispersal even when it was highly improbable. The fixed continent dogma was a costly lesson, but many did not learn it. After listening to papers at the XIV International Congress of Entomology at Canberra, 1971, and the First International Congress of Systematic and Evolutionary Biology in Boulder, 1973, I am convinced that many workers have dropped the dogma of fixed continents

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and adopted the new dogma of continental drift. Organisms whose dispersal is highly unlikely to have occurred by continental drift are now rationalized to have done so. It is time to drop all of our preconceptions and let the data suggest the most probable explanations.

Ross (1967) has noted that biogeography is only as meaningful as the accuracy of our interpretation of the phylogeny of the group. This is especially true for groups of widely disjunct distribution. I strongly believe that phylogeny can be reconstructed with reasonable accuracy even when the fossil record is scanty. As in all scientific inquiry, the various splits of a phylogeny diagram are hypotheses with varying degrees of probability and subject to constant testing with new data. The charge that phylogeny diagrams result from circular reasoning, that is, that phylogeny diagrams fit the data because they were generated from that data, has no validity if the group of organisms in question remains under active study. In the Ephemeroptera a number of workers are actively discovering new taxa, new life history stages, or new characters for known stages. Every such discovery presents the opportunity for testing one or more phylogenetic hypotheses.

The Ephemeroptera, most other insects, and many other organisms have various life history stages that have semi-independent genetic control, separate selection pressures and hence different rates of divergence. These differential rates of evolution in various stages are a powerful tool in the reconstruction of the sequence of branching in phylogeny. What should be equally apparent is that differential rates of semi-independent or independent character systems within a life history stage can provide equally powerful data. These facts are seldom consciously utilized by biologists. For example, adults of the mayfly families Caenidae (which are specialized), and Neoephemeridae (which are generalized) are so dissimilar that no known characters suggest that the Caenidae were derived from proto-Neoephemeridae.[3] But exoskeletal larval characters provide overwhelming evidence for this relationship (Edmunds *et al.*, 1963) and this is confirmed by the internal characters (Landa, 1969; for an opposing view, see Demoulin, 1958). Furthermore, Koss (1973) has demonstrated that the complex eggs of most Caenidae (some are of a more derived type) are identical to those of the genus *Potamanthellus* of the Neoephemeridae. This is very substantial evidence not only that Caenidae are derived from proto-Neoephemeridae, but

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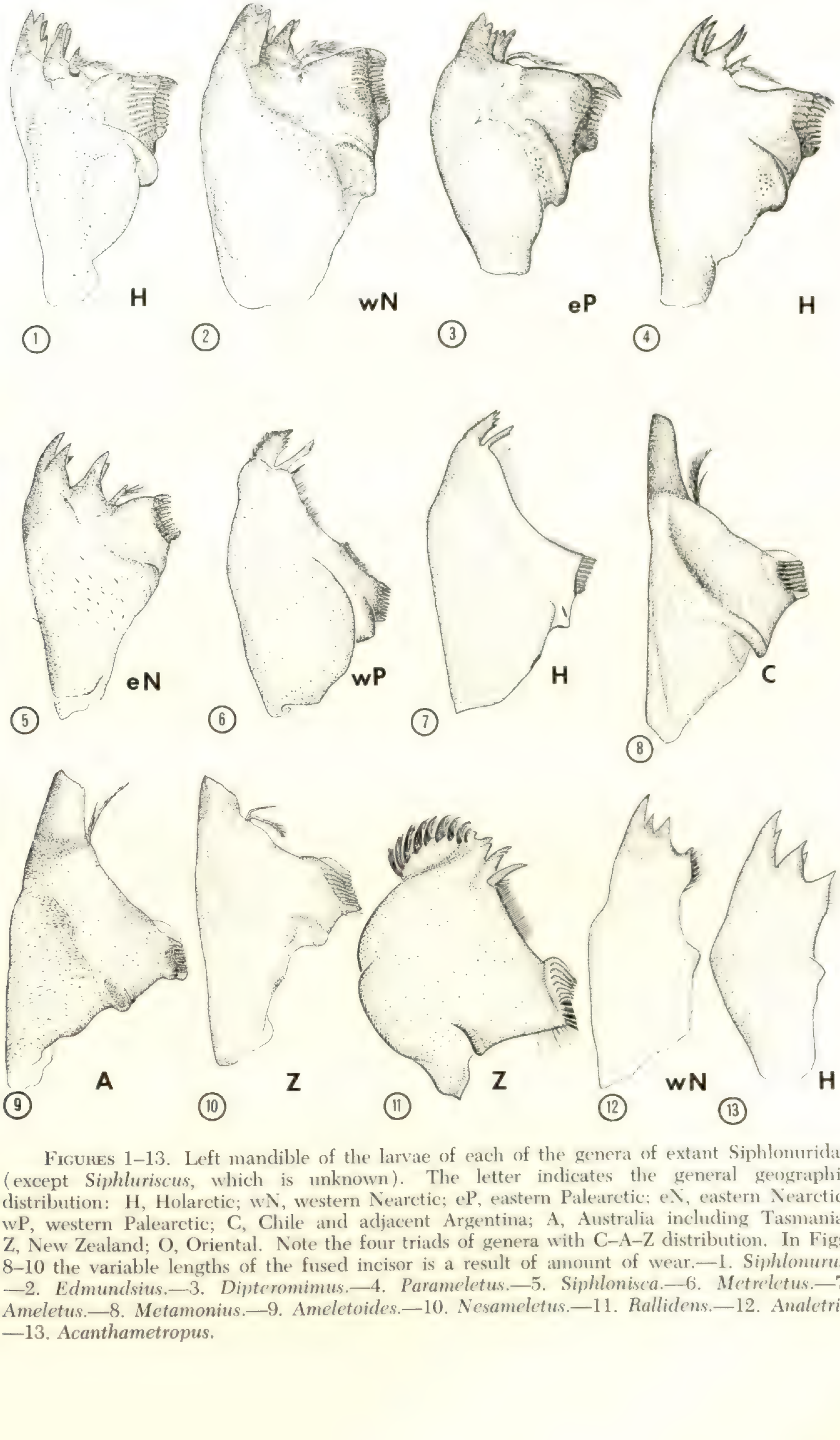
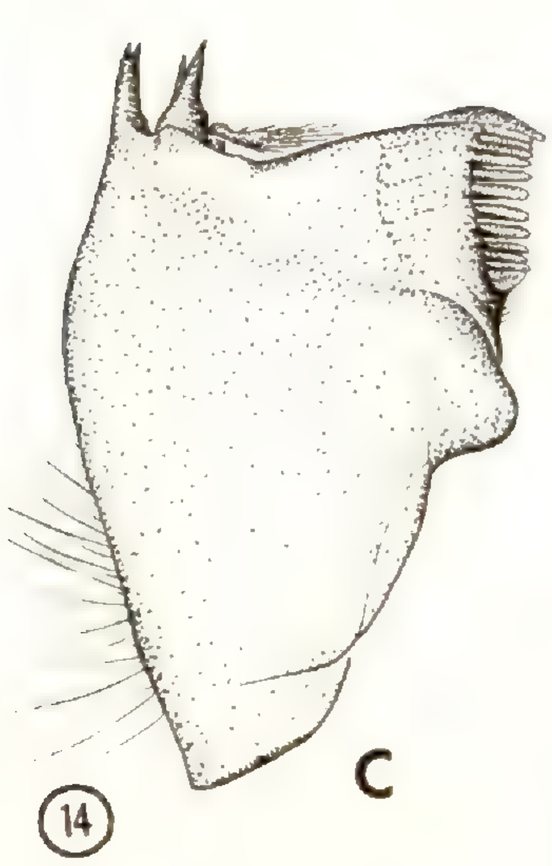
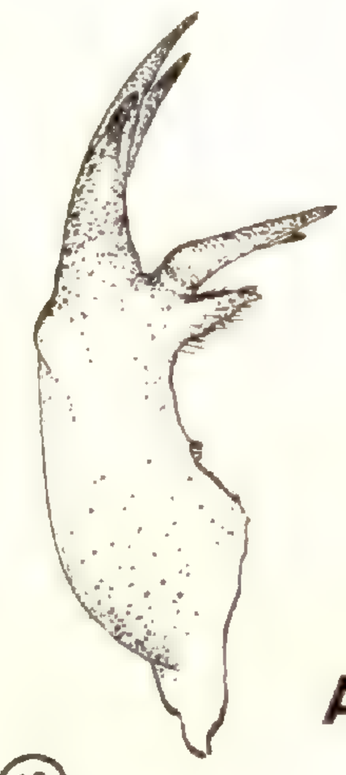
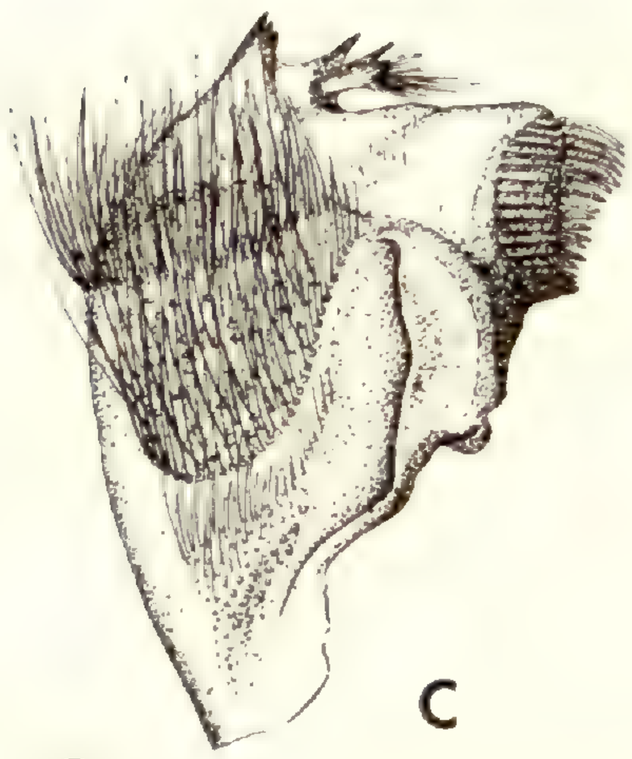
[3] In the terminology of the Hennig system the plesiomorphic Neoephemeridae are a sister group of the apomorphic Caenidae. From existing evidence I believe that the ancestors of many groups would be directly and unquestionably assigned to modern taxa if they were available to us. When I hold this opinion, I refer to the ancestors as proto-family x, or, in the example, proto-Neoephemeridae. If I believe that the ancestors did not have the characters of an extant group, I use the term pre-. For example, I believe that the ancestors of the Oligoneuriidae could have had all the characters of the extant genus *Isonychia*, but that the ancestors of the Heptageniidae were derived from an ancestor that also gave rise to *Isonychia*, and that several of the derived character states of *Isonychia* make it an extremely improbable model for the ancestral Heptageniidae. Hence I would refer to the ancestor of the Oligoneuriidae as proto-*Isonychia* and the ancestor of Heptageniidae as pre-*Isonychia*. I believe these to be in many cases more meaningful brief expressions than simply sister-group. By using such terminology we can avoid expressions such as "the Caenidae were derived from Neoephemeridae." We know that Caenidae were not derived from living Neoephemeridae, but in the case above a studied avoidance of such a statement seems to me to be "using water to wash duck's feet."

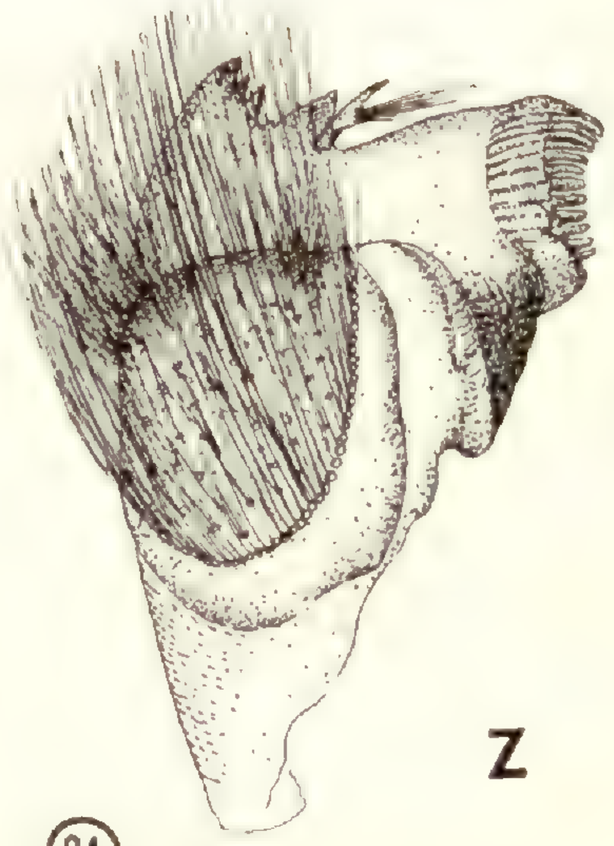


FIGURES 1–13. Left mandible of the larvae of each of the genera of extant Siphlonuridae (except *Siphluriscus*, which is unknown). The letter indicates the general geographic distribution: H, Holarctic; wN, western Nearctic; eP, eastern Palearctic; eN, eastern Nearctic; wP, western Palearctic; C, Chile and adjacent Argentina; A, Australia including Tasmania; Z, New Zealand; O, Oriental. Note the four triads of genera with C–A–Z distribution. In Figs. 8–10 the variable lengths of the fused incisor is a result of amount of wear.—1. *Siphlonurus*. —2. *Edmundsius*.—3. *Dipteromimus*.—4. *Parameletus*.—5. *Siphlonisca*.—6. *Metreletus*.—7. *Ameletus*.—8. *Metamonius*.—9. *Ameletoides*.—10. *Nesameletus*.—11. *Rallidens*.—12. *Analetris*. —13. *Acanthametropus*.









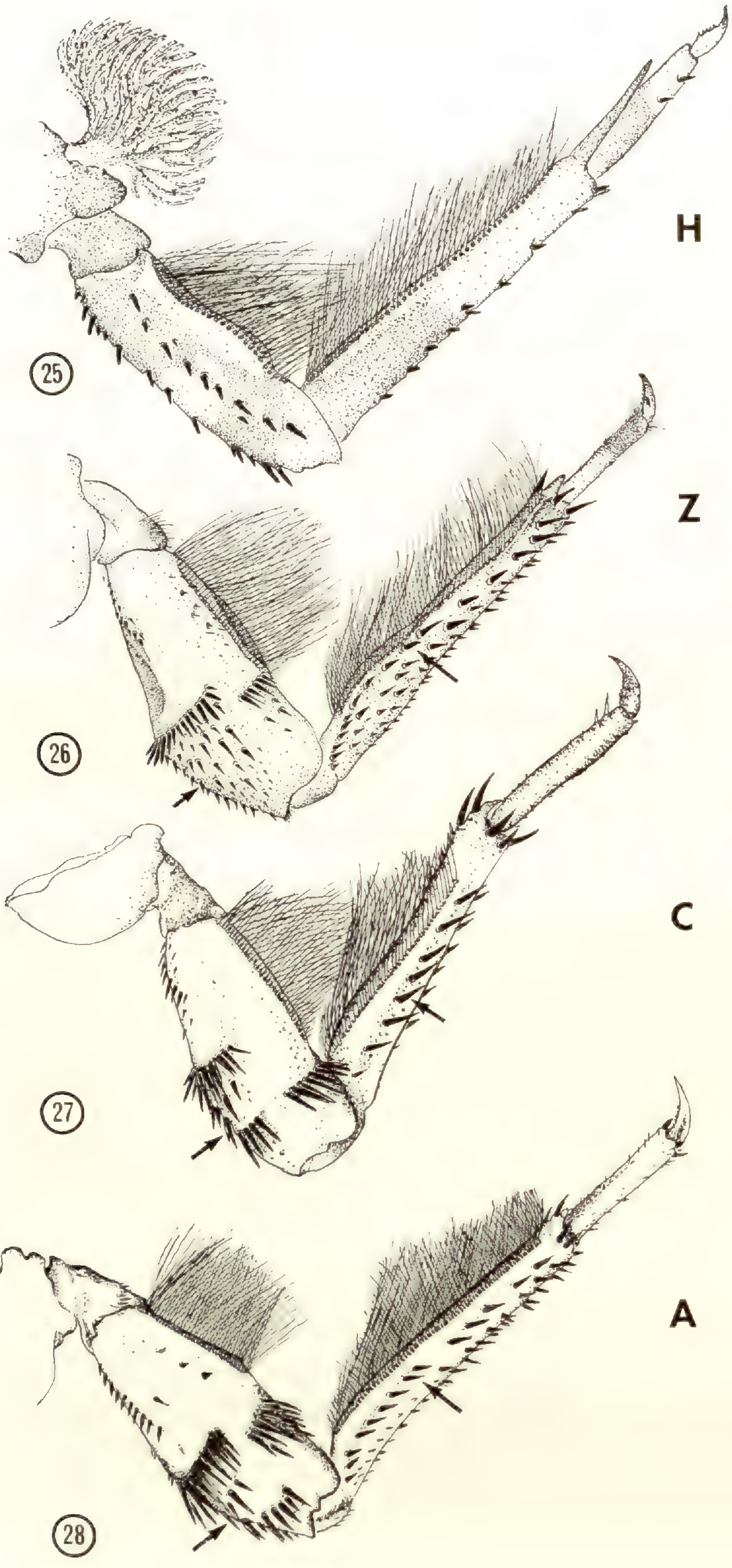
Figures 14–24. Left mandibles of larvae of genera of extant Siphlonuridae (continued). —14. *Siphlonella*.—15. *Tasmanophlebia*.—16. *Oniscigaster*.—17. *Chiloporter*.—18. *Chaquihua*. —19. *Mirawara*.—20. *Ameletopsis*.—21. *Isonychia*.—22. *Murphyella*.—23. *Coloburiscoides*. —24. *Coloburiscus*.

makes it clear that they were derived from a *Potamanthellus*-like member of the Neoephemeridae.

The clustering of organisms necessary for phylogenetic studies is done by grouping together those organisms with shared derived characters. Primitive characters may be scattered among the members of various distantly related lineages. Care must be used in determining which character states are specialized. There are some obvious clues. As noted, character states scattered widely among diverse lineages are likely to be primitive. Observations on behavior and function may make it clear which character states are primitive and which are derived. If one checks the distribution of a newly studied character against a reasonably good model of the phylogeny of a group, a wrong assumption of which character state is specialized likely will reveal a chaotic pattern, while the correct assumption is likely to lead to an orderly array on the diagram. For example, my early attempts at using wing venation for phylogenetic studies of mayflies failed to produce any reasonable pattern when I used the Comstock-Needham model of the primitive wing which assumes that intercalary veins have been added in the mayfly wing. The venational data became meaningful with the assumption that intercalary veins were primitive and a study of wing mechanics gave a plausible explanation of why the intercalary veins were originally important but were often subsequently reduced (Edmunds & Traver, 1954*b*). Nevertheless, there are cases when the decision of primitive or derived character states is not clear and such characters should be employed with considerable caution.

The primitive Siphlonuridae are generalist feeders and the mandibles are of a common type seen in many insects (Figs. 1–5, 14–16). Two derived lineages, Acanthametropodinae (Figs. 12–13) and Ameletopsinae (Figs. 17–20), are carnivores, and one lineage, Isonychiinae (Fig. 21) and Coloburiscinae (Figs. 22–24), has developed filter feeding. The clustering of the derived types from the mandibles alone (or from maxillae or labia alone) is obvious and the amphinotic distribution pattern appears four times (viz., Chile-Australia-New Zealand). The mandibles of one derived group (Figs. 14–16) are of the primitive type but there are numerous other shared derived character states in this group. The spur pattern on the legs of the filter feeders suggest that the Australian and Chilean forms are more closely related than the closely allied New Zealand form (Figs. 26–28, note arrows). The Holarctic filter feeder is more remote as shown by mouthparts, gills, and adult characters, but obviously of the same lineage.

In mayflies the primitive pattern in extant lineages is for similar gills on segments one to seven and each of the middle abdominal segments (segments 2–9) to be of about the same length. In *Oniscigaster* from New Zealand the structures are only slightly derived (Fig. 29). But note that in *Tasmanophlebia* (Fig. 31) from Australia and *Siphlonella* (Fig. 30) from Chile that the first gill is enlarged to cover and protect the other gills and that abdominal segments two to four are shortened to pull the gills under the protective gill on segment one. The Australian and Chilean member of the lineage burrow in the sand and the protective gill is a significant adaptation because the nymphs are hidden from predators and can exploit a habitat used by few other aquatic insects. According to McLean (1970), newly hatched *Oniscigaster* nymphs burrow, but as they grow, they move to the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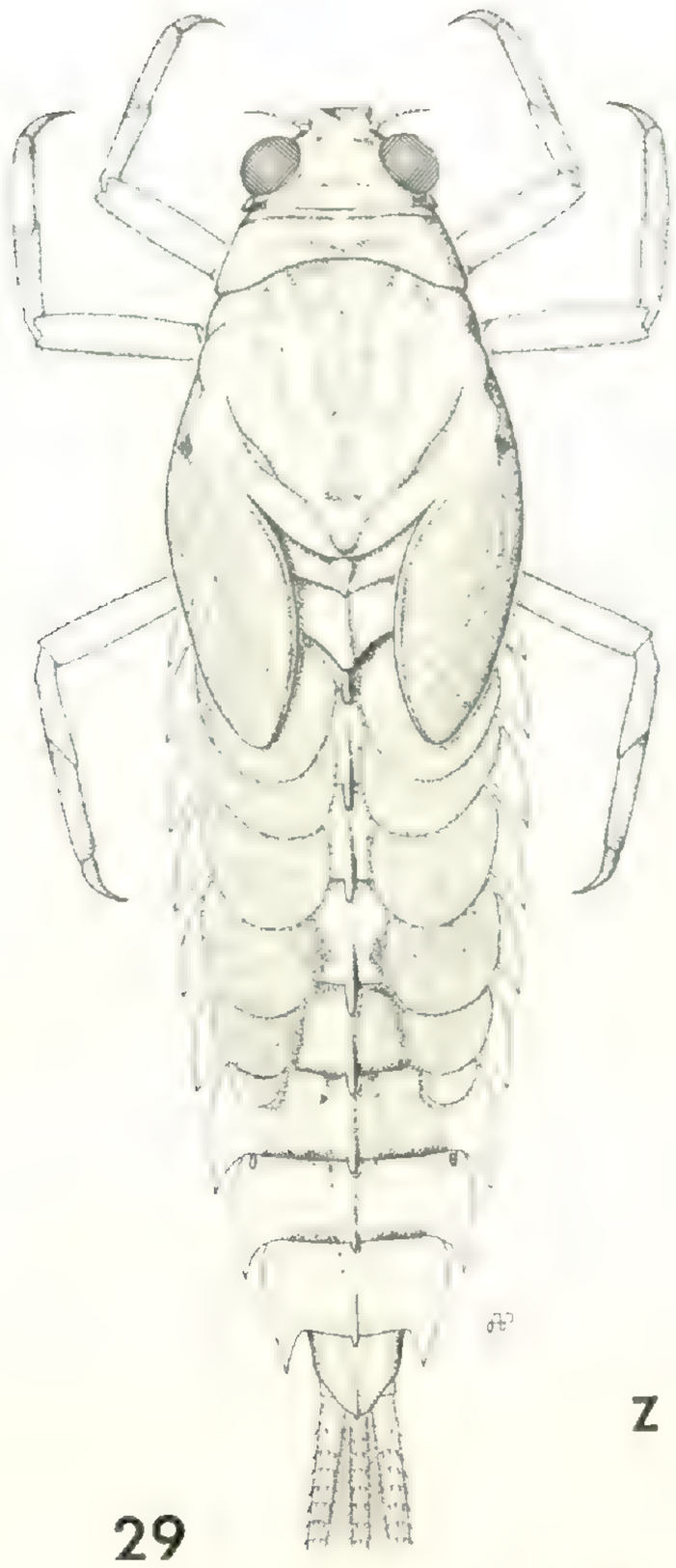

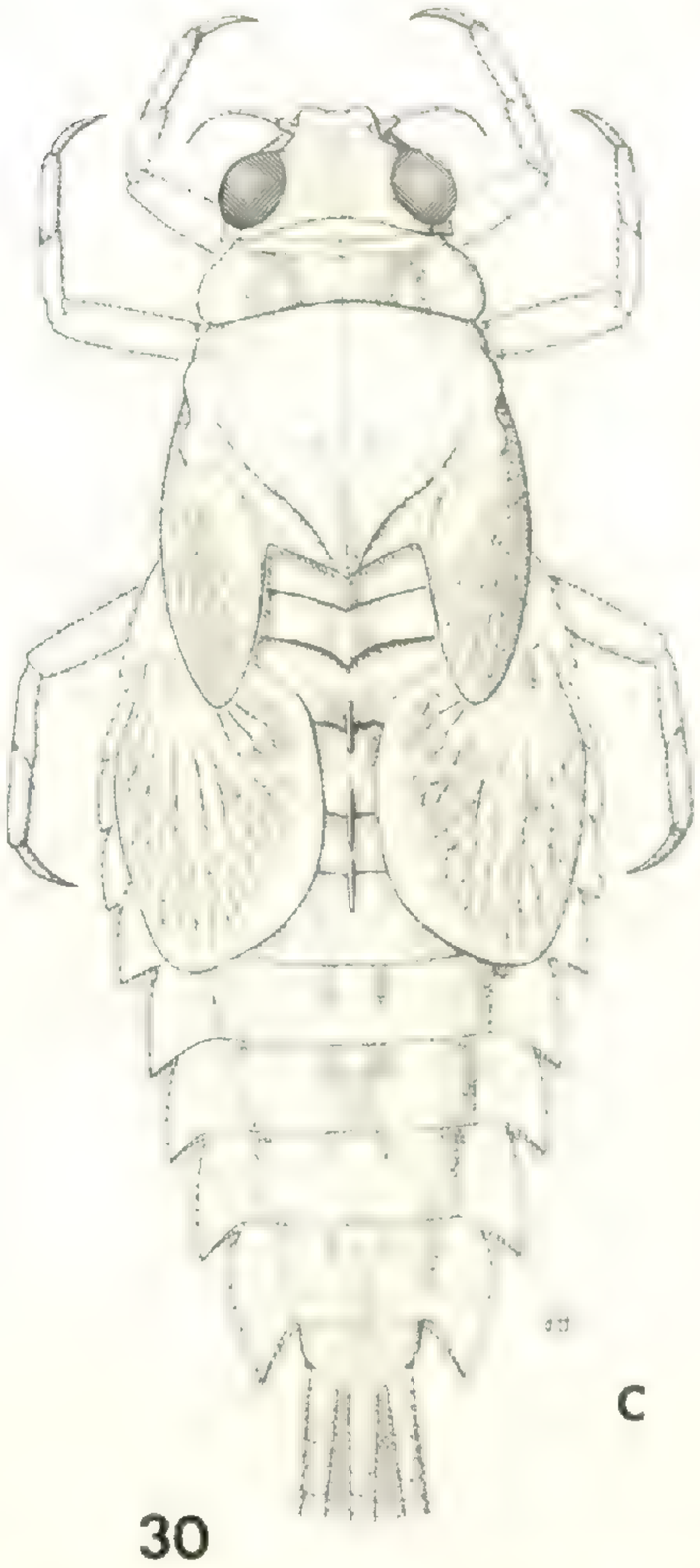

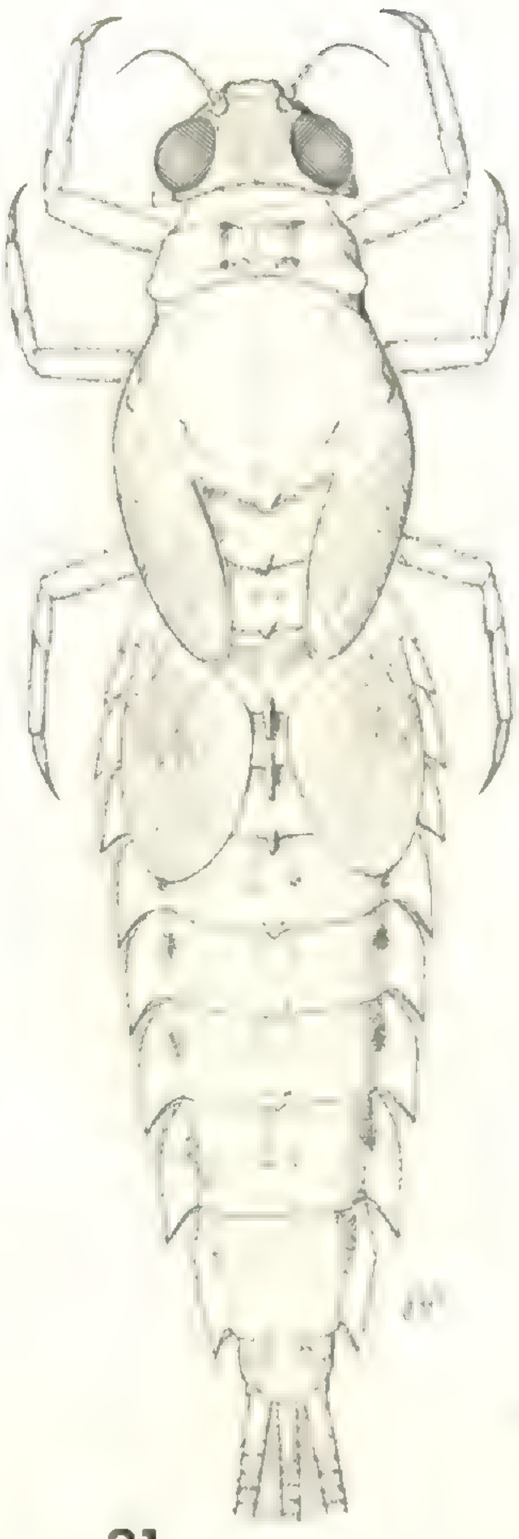

FIGURES 29–31. Larvae of Siphlonuridae. The letter indicates the general geographic distribution: Z, New Zealand; C, Chile and adjacent Argentina; A, Australia including Tasmania. Note that the C–A pair share the derived character states of gill 1 forming a protective plate (operculum) over the remaining gills and the shortening of abdominal segments 2–4 to bring the gills beneath the operculate gill. The modification is for burrowing in the sand.—29. *Oniscigaster*.—30. *Siphlonella*.—31. *Tasmanophlebia*.

surface, apparently because they lack the gill modifications necessary to allow them to remain in the sand as their surface to volume ratio reduces the relative area available for respiratory exchange. One sees in this example a combination of derived morphological and behavioral traits that almost certainly is a result of the origin of these two genera from a single species in which these traits had already evolved.

My geographically extensive field rearing of mayflies for the association of life history stages, has presented an opportunity to collect behavioral data, compare habitats and observe association with other kinds of organisms. Four lineages of ecologically associated mayflies of the family Siphlonuridae and several lineages

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FIGURES 25–28. Right foreleg of larvae of the filter feeding lineage, subfamilies Isonychiinae and Coloburiscinae. The letter indicates the general geographic distribution: H, Holarctic; Z, New Zealand; C, Chile and adjacent Argentina; A, Australia including Tasmania. Note the greater similarity of spur patterns of the A–C distribution pair, with Z as the sister group, and H a sister group of the A–C–Z triad.—25. *Isonychia*.—26. *Coloburiscus*.—27. *Murphyella*.—28. *Coloburiscoides* (see also Figs. 21–24).

of Leptophlebiidae are represented by at least one genus in Chile and neighboring Argentina, one in Australia and another in New Zealand. Similar patterns are seen in associated stoneflies, caddisflies, midges, the unique aquatic larvae of the nannochoristine Mecoptera, and other aquatic insects. Whole communities of aquatic insects are seen to show the same geographic pattern. This pattern suggests strongly the past division of a single biota.

It is obvious that certain lineages of mayflies are exceptionally good material for phylogenetic biogeography. By using multiple character systems from egg, larval, and adult stages, the traditional lines between higher taxa begin to blur, but phyletic lines become more and more clear. This complex of data has allowed repeated testing and refinement of phylogenies of some lineages so we have considerable confidence that we have good phylogeny data and hopefully have avoided the pitfall of parallelism. (Obviously one cannot *know* of undetected parallel evolution.) For some mayflies our information is meagre. The family Baetidae is poorly known and the family Leptophlebiidae, although the subject of intense investigation by several workers and of immense biogeographic interest, is almost overwhelming in its size, complexity, and number of undescribed genera.

The widely-used methods of systematic biology define higher taxa on the basis of common characters that differentiate such taxa. Therefore, extant primitive forms that are phyletically close to a given taxon may be in another genus, subfamily or family. In addition, there may be living derivatives excluded from the given taxon. Hence, in biogeographical study, the analysis of the distribution based on taxa clearly can be misleading. Therefore, I concern myself with the biogeography of phyletic lines, not of taxa, because any taxon may be defined so as to exclude primitive members, its derived members, or both. This can result, then, in phyletically close forms of key biogeographic interest being excluded from or misplaced in the biogeographic analysis.

Some examples will clarify this. The mayfly family Siphlonuridae is widely distributed in the Holarctic and Oriental Realms and in the Southern Hemisphere from Chile and adjoining Argentina, Australia, and New Zealand. One small lineage of this family includes two small subfamilies. One subfamily for the genus *Isonychia* ranges widely over the Holarctic and is the only genus of siphlonurid mayflies in the Oriental Realm (one species also is found in Central America). The other small subfamily shares the southern distribution noted above with a number of other siphlonurids. But an *Isonychia*-like ancestor has given rise to a derived family, the Oligoneuriidae, whose distribution fills much of the intervening tropics and has spread back to the temperate regions. If I am correct in my preliminary assessment of the biogeography of this family, it evolved on the South America-Africa-Madagascar-India land mass. The genus *Chromarcys* is the most primitive oligoneuriid. It is found in Ceylon, Thailand, South China, and Sumatra. But the nymphs of *Elassoneuria* of Madagascar and Africa are very *Isonychia*-like in behavior and structure and are the most primitive of the subfamily Oligoneuriinae. An *Isonychia*-like mayfly apparently entered Gondwanaland, where the adults differentiated to the degree that these mayflies are placed in another family. Thus the lineage would be disregarded in assessing the biogeography of the Siphlonuridae. Or, assessment of the biogeography of the Oligo-

neuriidae would certainly have excluded *Isonychia* and many would have excluded the very critical *Chromarcys* because it too is often excluded taxonomically from the Oligoneuriidae. Edmunds & Traver (1954*a*) first placed *Chromarcys* in the Oligoneuriidae and some other workers disagree with our decision (*e.g.*, Demoulin, 1967). I believe that I am quoting H. H. Ross that genera such as *Isonychia* and *Chromarcys* are "the taxonomist's nightmare and the phylogenist's dream."

On the basis of detailed study, three mayfly workers (Edmunds, 1973; Landa, 1973; McCafferty, 1972) more or less simultaneously arrived at the conclusion that within the present family Ephemeridae we could identify a few genera that shared derived character states with the Palingeniidae, thus correcting the earlier misplacement of the Palingeniidae near the Polymitarcyidae. McCafferty (1972) singled out the genus *Pentagenia* and placed it as intermediate between the two families and in a new family. Later, my field work in Madagascar led to the association of adults and larvae of another genus that makes it abundantly clear that the most palingeniid-like ephemerid or ephemerid-like palingeniid is the North American *Pentagenia*. The Palingeniidae are all Old World, with the most primitive members in Madagascar and India. One is tempted to suggest that the North American-Madagascar dispersal dates back to Pangea with extinction in Africa. In any case, the biogeography of neither the Ephemeridae nor the Palingeniidae is clear without considering the phyletic lines, rather than the taxa.

Some may be tempted to wonder if such taxonomic problems in mayflies are not the result of previous fragmentary knowledge. But, in fact, the taxonomic problems increase in proportion to the knowledge of characters and life history stages. The very same kinds of problems have arisen in avian taxonomy with the study of new characters in adults, the downy young, and egg albuminoids.

Fossils are highly desirable for phylogenetic study. In the mayflies they have provided approximate dates of the appearance of certain taxa, indicated some geographic areas where lineages have become extinct, and the Baltic Amber fossils give a fair idea of a former local mayfly fauna and its grade of evolution. Directional trends of some characters, especially of wings and venation, are confirmed by fossils. The most critical fossils are those that are intermediate between major taxa. The genus *Isonychia* is known from the Miocene of Montana. While assigned to the Siphlonuridae, it clearly is intermediate as a nymph between Siphlonuridae and Oligoneuriidae. As noted, *Isonychia* is a widespread extant genus. In all probability *Isonychia*-like mayflies had evolved before the Cretaceous, and fossils are now *known* to be possible from Miocene to the present. Many (but certainly not all) taxonomists and biogeographers are aware that the occurrence of a fossil by a certain time means only that a group had evolved by that time. Fossil evidence becomes highly probable for dating the splits in phylogenies only when a significant variety of fossils is known. *Isonychia* is as remarkable a "living fossil" as *Latimeria*, but the mayflies appear to be replete with "living fossils." This is to be expected in small organisms that can pack many species into a general habitat.

Some biologists have written emphatically about absolute dependence on fossils

for studies of biogeography and phylogeny. I believe that acceptance of this statement has hindered the progress of phylogenetic biogeography. Colbert (1973) has repeated these warnings concerning Gondwanaland. He states, "There are too many complex factors of animal and plant distribution—the result of earth history since Permo-Triassic times—for modern organisms to be interpreted as indications of ancient Gondwanaland relationships, except with the utmost circumspection. Darlington, whose wide-ranging studies in the biogeography of both modern and extinct organisms are noteworthy by reason of the thoroughness and careful interpretations with which they have been made, has suggested that 'plant and animal distributions as now known do not show where the earlier connections were. Only in the late Cretaceous and especially in the Tertiary do plant and animal distributions begin to show specific land connections and specific ocean barriers, and this is too late to be significant in any likely hypothesis of continental drift' (Darlington, 1965: 197). Such being the case, our attentions will be directed, as they have been, to the fossil forms." But a careful analysis of Colbert's proofs for continental drift through the distribution of fossil *Lystrosaurus*, *Mesosaurus* and *Cynognathus*, shows that except for the fact that these genera are known only as fossils, his methods are exactly those of a biologist studying living organisms. He has the disadvantage of few characters to study and the advantage that he need not be concerned about later invasions. Fossils and their study are extremely important, but some paleobiologists need a broader perspective about phylogenetic methods.

All of us would like to find an ideal group of organisms for given biogeographic studies. I will outline the characteristics of the *ideal group* because I think it helps point out common errors by biogeographers. Let us assume that we want to know the history of the breakup of Pangea. Our ideal organism should have been as follows.

1. It was a single species that had relatively recently spread over all of Pangea.
2. As the population was split by the breakup of Pangea, all segments evolved at a uniform rate.
3. No extinction took place on any of the segments of land.
4. Modern biologists must collect these organisms on all remnants of Pangea and study enough characters that the phylogeny can be constructed in acceptable detail.
5. Some fossils should be present for dating of the sequence.

If, of course, unambiguously datable fossils were left behind at critical phases of evolution at places where paleobiologists would have access to them, dig them out, recognize them, and get them in the hands of the proper authority, we could do with fewer restrictions.

Obviously, there are no organisms that fit the criteria I have outlined. In fact, most will not fit any of the rules, but this is not a hollow exercise.

I have suggested that Australia and southern South America were more recently connected (via Antarctica) than was either to New Zealand (also see Mackerras, 1970). Some of my critics point out that I must be wrong since there are single genera found in Chile and New Zealand but not in Australia. But I can be proved

wrong only if we assume that evolutionary splits did not take place prior to the land disruption and that the organism was on that part of Gondwanaland that became Australia (see ideal organism characteristic 1), that the Australian members did not evolve faster and are now excluded from the taxon (see 2), that extinction of the lineage in Australia did not occur (see 3), and that the group has been collected in Australia if it is still extant (see 4).

I am particularly concerned about the number of biogeographers who have anguished over the problem of the absence of organisms that "should be in an area" if there was a land connection. Yet these same workers obviously know better and none would defend the concept of prior uniform distribution of a single species on land masses.

Everyone knows that evolution rates vary, yet we continue to do most biogeographic analyses on the basis of taxa which are defined on the basis of their differentiation rate. A purely cladistic systematic arrangement is the ideal for biogeographers but I am dubious that it will serve other needs of taxonomy. In any case, I find it unnecessary purely for purposes of biogeography to obfuscate the continum of evolution by applying the discontinuity of any system.

The assumption of extinction is a nice way of making certain geographic problems simpler but it is pure speculation in the absence of fossils. Nevertheless, sometimes the assumption that extinction of a specified group took place on a certain land mass seems overwhelmingly logical. The mayfly family Siphlonuridae is unknown either fossil or living in Africa and Madagascar but is represented in Australia, New Zealand (but not New Caledonia), and southern South America by four cool-adapted subfamilies (with a fifth in New Zealand only). I feel safe in speculating that this family was in Africa, and will express no surprise if it is discovered in Africa or Madagascar, either living or fossil. Furthermore, there are lineages derived from the Siphlonuridae in Africa and Madagascar that could represent a faster-evolving lineage of the family (although it is equally likely that the derivation took place elsewhere). Despite the dangers of assumed extinction, the possibility must enter into the reasoning process.

Negative evidence, *i.e.*, the lack of evidence of the presence of a group on a land mass (either fossil or extant) has been repeatedly misused by biogeographers. For extant groups, its validity obviously depends on the degree to which the group has been studied.

Even though the "ideal group" doesn't exist, among the many groups that have been separated by continental drift or the origin of other barriers, biogeographers must utilize the data from those phyletic lineages present as three or more phyletically related geographically disjunct populations that seem to fit as closely to the ideal as possible. The detection of these groups appears to lie in comparisons of numerous lineages in biotas that have been disrupted by such barriers.

I have summarized much of the biogeography of major groups of the Ephemeroptera (Edmunds, 1972). Briefly, my findings were that the present distribution of the mayflies shows considerable evidence of continental drift. Furthermore, in the Southern Hemisphere some of the groups provide good data for the sequence of the breakup of Gondwanaland. I believe that the last major land connection in the Southern Hemisphere was the connection of South America

to Australia via Antarctica. There is abundant biological evidence that the land mass that includes New Zealand and New Caledonia had already been separated from the larger land mass. Many cool adapted insects present in New Zealand are absent in New Caledonia. They may have become extinct, but it is just as likely that their absence and some of the floral similarities of New Caledonia and Australia represent latitudinal zonation patterns.

Still earlier, I believe that Africa-Madagascar-India had broken away from Gondwanaland separating first in the south and moving away from South America in a motion that left the last connection between the two land masses near the equator. I have been able to further study my collections from Madagascar and several collections from Ceylon and have good evidence that India and Madagascar remained as a single land mass after they broke from Africa. Some of these Madagascar-India elements are also found in Southeast Asia. I do not think that it is necessary to suppose that Borneo or any other part of Southeast Asia was part of Gondwanaland. The leading edge of drifting India must have provided an excellent entry for a number of faunal elements to Southeast Asia and perhaps to the Middle East. The mayfly genus *Prosopistoma* which is diverse in Africa has one species in Madagascar and a series of species stretching from Ceylon east to the Philippines and New Guinea. The Oriental species group appears to be a tightly-knit one that probably represents the speciation of an original single species that entered with the Indian land mass. The genus *Neurocaenis* (Tricorythidae) has a similar pattern, as do the heptageniid genera *Compsoneuriella* and *Thalerosphyrus*. The latter two genera may have dispersed in the opposite direction, *i.e.*, from Southeast Asia to Africa and Madagascar. The biogeographical relationships of Southeast Asia, Africa and Madagascar are complex and more study of these biotas are necessary before our conclusions have a high probability of being correct. The very important and diverse mayfly families Leptophlebiidae and Baetidae are incompletely studied in these areas.

It is obvious that certain mayfly lineages evolved primarily in the Africa-South America-Madagascar-India mass. For the Asthenopodinae (Polymitarcyidae), Tricorythidae, Oligoneuriidae, and Baetidae this appears to be the major center of evolution. The Leptophlebiidae are also involved but this is an old group with several major lineages and their evolution must be followed as several complex lines. Groups such as the Oligoneuriidae and Tricorythidae have relatively simple patterns with North American members of the family derived from South America and Eurasian forms probably derived from the Africa-Madagascar-India area. One important pattern is evident in the Holarctic and Oriental derivatives of this southern land mass. In the New World these derivatives are, as far as I know, always congeneric with South American genera (*e.g.*, *Lachlania*, *Homoeoneuria*, *Tortopus*, *Campsurus*, *Traverella*, *Homothraulus*, *Baetodes*, *Dactylobaetis et al.*). The taxonomic situation in the Old World appears to be much more complex, suggesting that entry into the Palearctic and Oriental areas took place at various times and at various points. In some cases we find congeners (*Povilla*, *Neurocaenis*, *Oligoneuriella*, *Prosopistoma*) and in other cases there are obviously related lineages (in the Baetidae, the teleganodine Ephemerellidae, Oligoneuriidae and

the Euthyplociidae) where the similarity does not extend to the congeneric level. Unfortunately, tropical mayfly collections and studies are grossly inadequate.

Several mayfly genera and species groups such as *Arthroplea*, *Metretopus*, *Ametropus*, *Parameletus* and *Baetis* are consistent with the expansion of the Atlantic. The mayflies of the Northern Hemisphere are well known except for those of China and Asian U.S.S.R. but the detailed studies necessary for assessment of dispersal routes has not had sufficient attention by mayfly workers to date.

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SOME ASPECTS OF PLANT GEOGRAPHY OF THE NORTHERN HEMISPHERE DURING THE LATE CRETACEOUS AND TERTIARY

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ABSTRACT

Palynological data emphasize the presence of two distinctive provinces during the Late Cretaceous, one including eastern North America and Europe and a second including the major part of Asia and western North America. The distinction between these two provinces became increasingly blurred during the Paleogene. During the Eocene, the rain forests of both Europe and western North America shared numerous genera, both extinct and extant. The great majority of the latter and most of the closest extant relatives of the former now occur in the Indomalayan region. It is thus clear that much of the present Indomalayan flora represents a relict of a once widespread Northern Hemisphere tropical (s.l.) flora, one that has largely (but not entirely) been eliminated from the New World. Among the possible New World survivors of this boreotropical flora are some of the dry Caribbean genera, which could have been derived from lineages of the dry tropical vegetation of the Gulf Coast Eocene; only a handful of present Neotropical lowland rain forest genera appear to be boreotropical relicts.

Much has been postulated concerning the historical biogeography of the floras of the Northern Hemisphere during the Cretaceous and Tertiary (*e.g.*, Chaney, 1940; Takhtajan, 1969), but many of the suggested migrations and many of the suggested relationships have either turned out to be based on serious misinterpretations of the ages of various fossil floras or on invalid determinations. Paleobotany, particularly that of the angiosperms, has in recent years been undergoing radical changes. The increasing amount of palynological information has contradicted many concepts based on megafossils (particularly foliage; *cf.* Wolfe, 1973), and this has in turn led to reevaluation of some of the fundamental approaches to angiosperm paleobotany (Weber, 1972). In the present report, I will attempt to summarize some of the paleobotanical data that appear to be reliable. From these data, certain tentative conclusions can be drawn concerning ancient floristic relationships; combined with data derived from analyses of the present distribution of some angiosperm groups, hypotheses can be ventured, but I emphasize that many of these hypotheses require confirmation or rejection from future work.

One concept that has particularly influenced some current interpretations of historical biogeography of plants is that of the "Geoflora" (Chaney, 1959). Based originally on the "arcto-tertiary" concept, the geofloral concept was expanded to the "Neotropical Tertiary Geoflora" and the "Madro-Tertiary Geoflora," among others. As has been discussed elsewhere (Wolfe, 1969*a*, 1972), the concept of an "Arcto-Tertiary Geoflora" was based on highly erroneous assumptions regarding the ages of various high latitude plant assemblages. In regard to the "Neotropical Tertiary Geoflora" concept, however, fossil determinations probably have been highly inaccurate. That is, the bulk of the fossil megathermal to mesothermal

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leaf-species determined in western North America in the first part of this century were assigned to genera now exclusively neotropical or were thought to be related to neotropical species in the instances of genera both neotropical and paleotropical (*e.g.*, Chaney & Sanborn, 1933). MacGinitie (1941), however, validly determined a large number of paleotropical elements in the California Eocene. Even more significantly, the only large fructification flora from the Pacific Coast Paleogene has been shown to be overwhelmingly paleotropical (Scott, 1954, and *in* Chandler, 1964: 58), and this calls for a reevaluation of the many leaf imprints of putative neotropical affinities.

One of the basic foundations of this discussion is that the angiosperms are basically of Cretaceous origin and that certainly the major diversification of the angiosperms occurred during the Cretaceous (Doyle, 1969; Wolfe *et al.*, 1975). Thus, the distribution patterns now present in the angiosperm flora are a reflection of events that occurred primarily during the Late Cretaceous and the Cenozoic. These events that directly affected angiosperm distribution fall into two main categories: geographic and climatic. Less controversy surrounds interpretations of the geographic positions of the Northern Hemisphere continents relative to one another than for Southern Hemisphere continents. In regard to paleoclimatic interpretations of the Tertiary, some controversy does exist (Axelrod & Bailey, 1969; Wolfe, 1971), and little paleoclimatic data are available for the Cretaceous.

The Tertiary period is traditionally divided into two major units: the Paleogene and the Neogene (Fig. 1). From the paleobotanical and paleoclimatological record, however, a more meaningful two-fold subdivision of the Tertiary would be by the major climatic deterioration of the Oligocene (ca. 31–32 m.y.; *cf.* Wolfe & Hopkins, 1967; Wolfe, 1971). Prior to that deterioration, Tertiary climates were characterized by high equability (*i.e.*, a low mean annual range of temperature; *cf.* Berry, 1914; MacGinitie, 1941; Traverse, 1955) and, during some periods, high levels of warmth (*i.e.*, high mean annual temperature) to high latitudes (Wolfe, 1971, 1972). The Oligocene deterioration resulted in a major increase in mean annual range of temperature concomitant with a major decrease in mean annual temperature.

The use of the terms "megatherm," "mesotherm," and "microtherm" in this discussion follows that of de Candolle (1874) with one modification. While accepting a mean annual temperature of 20°C as separating megatherms from mesotherms, I prefer to place the mesotherm-microtherm boundary at 13°C rather than the 15° proposed by de Candolle. To accept the higher figure would mean that the broadleaved evergreen forest of an area such as Japan would be mesothermal in some areas and microthermal in other areas (*cf.* Wolfe, 1971: fig. 5).

Reasoning from Fossil Distributions

One particular example of how the fossil record can assist in clarifying the problems in historical biogeography is Bombacaceae. Today, the family has its greatest generic and specific diversity in South America. Additionally, some African genera have close relationships to some South American genera, but some African genera also extend into the Indomalayan area. Such a distribution could

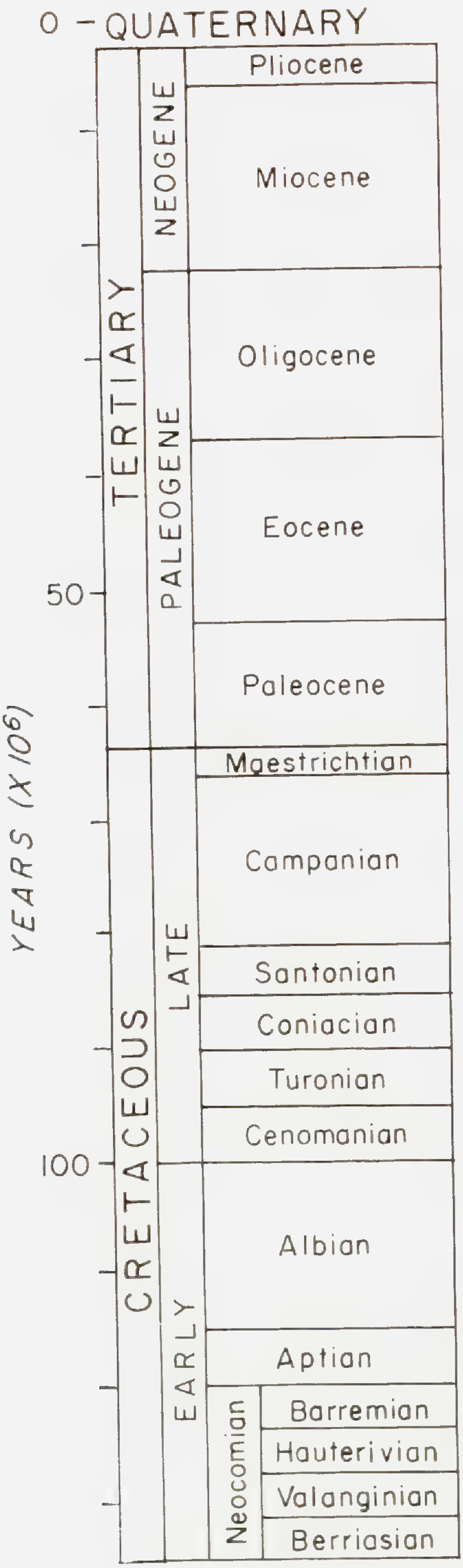
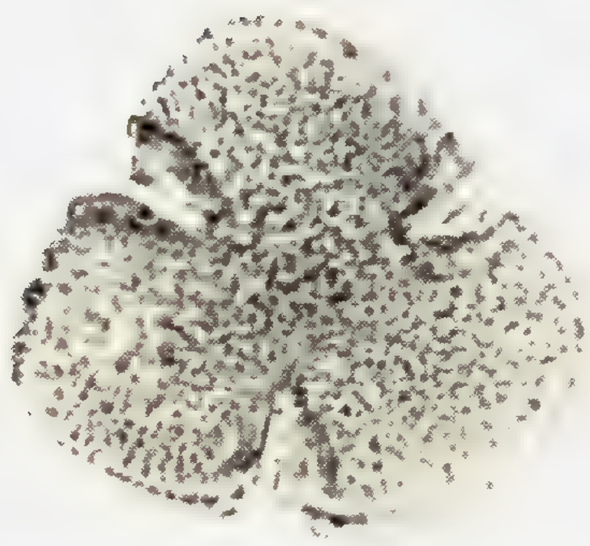


FIGURE 1. Approximate duration of Cretaceous stages and Tertiary epochs (from Wolfe, 1973).



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FIGURES 2–4. Pollen from the Upper Cretaceous of the Atlantic Coastal Plain of the eastern United States. All figures ×1,000.—2. Bombacaceae, USGS Paleobot. loc. 11223-B, upper part of Navesink Formation (basal Maestrichtian), Atlantic Highlands, New Jersey.—3. USGS Paleobot. loc. 11219-B, lower part of Merchantville Formation (lower Campanian), Oschwald Pit, New Jersey.—4. USGS Paleobot. loc. 11067-B, Cliffwood beds of Magothy Formation (basal Campanian), Cliffwood, New Jersey. The pollen grains illustrated in Figs. 3–4 are closely spaced stratigraphically, whereas the bombacaceous pollen (Fig. 2) is approximately 20 million years younger than the pollen in Fig. 3.

be interpreted to reflect an origin in Gondwanaland, and the Indomalayan genera as reflecting later dispersal from Africa.

In South America, the earliest occurrence of the *Bombax ceiba* type of pollen is in the Paleocene, but, as Germeraad *et al.* (1968: 277) have pointed out, ". . . the rather sharp lower level of occurrence suggests immigration from elsewhere." The elsewhere was not Africa, because this pollen type first occurs somewhat higher in the section than in South America.

Palynologically, the *Bombax ceiba* type is at a higher grade of specialization (size, sculpture) than other related Bombacaceae (*e.g.*, *Spirotheca* and *Cavanillesia*). Insofar as I am aware, the oldest certain record of Bombacaceae is not in South America but is from the lower Maestrichtian of New Jersey, where pollen highly similar to that of *Cavanillesia* has been found (Fig. 2). Even earlier (in the early Campanian) in this area, pollen that has the same type and location of apertures and shape of grain as in this group of Bombacaceae is encountered (Fig. 3); the sculpturing, however, is simpler than in any extant member of this group of Bombacaceae and the size is also smaller. Yet earlier (in the Santonian and earliest Campanian) is an even smaller and smoother grain (Fig. 4) that also has the basic pattern of shape and pore location of this group of Bombacaceae. In contrast with the sudden entry of advanced types of the family in the South American pollen record, apparently ancestral types occur throughout a 20-million-year span of time in eastern North America. Fuchs (1967) suggested a triphyletic origin of the family, but I think it equally feasible that from eastern North America the family spread into the ancient Aquilapollenites province during the Paleogene, developing a pollen type different from the *Bombax ceiba* type (*i.e.*, the *Durio* type), a relict of which is left in North America (*Huberodendron*). In Asia, the *Durio* type evolved further into the *Adansonia* type, which spread southward into Australasia and westward into Africa and finally reached South America. Thus, the South American Bombacaceae may represent three basically different groups within the family and arrived at three different times: the *Bombax* type in the Paleocene from North America, the *Durio* type at a later date but also from North America, and the *Adansonia* type from Africa.

THE LATE CRETACEOUS

One of the most striking features of the Northern Hemisphere Late Cretaceous floras is the pronounced floristic difference between the Normapolles and the Aquilapollenites floras. The Normapolles group was dominant in the Late Cretaceous of the eastern United States and Europe. The affinities of this largely extinct group in terms of extant plants has been the subject of much discussion, but increasingly the evidence indicates that several of the so-called amentiferous families, *e.g.*, Juglandaceae, Ulmaceae, and perhaps Betulaceae, were derivatives of the Normapolles stock (Doyle, 1969; Wolfe, 1973). Although the abundance of pollen of the Normapolles group might be an indication of wind pollination, as is the case in the probable survivors of that complex, this applies only to a few of the Normapolles genera in the eastern United States, viz., *Trudopollis*, and *Pseudoplicapollis*. The great majority of Normapolles genera are heavy walled and thus presumably unsuited to wind transport, a suggestion also supported by the rarity of such pollen types in individual samples. There is thus no reason to suspect that the majority of the Normapolles genera were similar in habit or habitat to the few wind-pollinated descendant families.

Despite the fact that Normapolles genera dominated in both Europe and eastern North America, considerable differences are apparent between these two areas. Some Normapolles genera are, of course, common to the two areas, but many are not. Considering the possibility that a pollen genus may well be equivalent to a suprageneric group and that pollen species are typically equivalent to genera, the floristic differences between Europe and eastern North America from at least the Coniacian through the Campanian are significant. There appears to have been little floristic interchange between middle to low latitude regions on either side of the North Atlantic following the Cenomanian until the Maestrichtian.

What the barrier was to interchange is uncertain. The evidence points to the probability that the Normapolles group was largely thermophilic (Wolfe, 1973), and thus the differences between the European and North American members of this group may be largely due to an inability to migrate through the more temperate climates at higher latitudes.

During the later part of the Late Cretaceous, some Normapolles genera are known in western North America and Siberia, but these are few. As noted by many others (*e.g.*, Góczán *et al.*, 1967), this other area constitutes a distinct floristic province characterized by pollen types such as *Aquilapollenites* and *Wodehousia*. Interestingly, Muller (1968) has recorded *Aquilapollenites* from the latest Cretaceous of Borneo, thus placing the Indomalayan region west of Wallace's Line in the Aquilapollenites province. In contrast, the latest Cretaceous of Africa and South America have their own pollen flora distinct from that of either Northern Hemisphere provinces.

I do not mean to imply that there was a total lack of floristic interchange between the Normapolles and Aquilapollenites provinces. Although extremely rare, *Aquilapollenites* has been encountered in samples from the middle Atlantic States and some Normapolles genera are found in western North America and

Siberia. In general, however, the two regions were effectively isolated floristically. It is not difficult to suggest a reason for these distinctive provinces—their boundaries coincide with the epicontinental seaways that occupied the present sites of the Urals and the High Plains of North America.

Some floristic interchange between the Northern and Southern Hemispheres has been indicated by the occurrence of putatively proteaceous pollen in Northern Hemisphere regions. I can now demonstrate, however, that the so-called *Proteacidites* from eastern North America is in fact a Normapolles derivative that is only convergent with proteaceous pollen, a confirmation of Tschudy's (1971) suggestion. Of course, much podocarpaceous and araucarian pollen is found in the Northern Hemisphere Cretaceous, but such pollen types had the same distribution in the Cenomanian or earlier times.

The Paleogene

During the Paleocene and Eocene, the Normapolles group—at least the more basic types—became extinct. Further, various pollen types—both Normapolles and other types of angiosperms—that had been previously restricted to Europe or to eastern North America appeared in the other's subprovince near the Cretaceous/Paleocene boundary. Just as significantly, both megafossil and microfossil data indicate a definite blurring of the distinction between the Normapolles and Aquilapollenites provinces. By the Eocene, the flora of Europe became highly similar to that of western North America, with numerous genera common to both areas.

As opposed to the present floristic kingdoms of the world in which the division in the tropical flora is rather pronounced between neotropical and paleotropical, during the Paleogene the division was more pronounced between the Northern and Southern Hemispheres, that is, a boreotropical kingdom versus an austrotropical kingdom.

The routes by which this boreotropical flora became distributed are not certainly known. One route certainly appears to have been the high latitude Beringian connection between Eurasia and North America (Wolfe, 1972). Fundamentally megathermal families and genera have been recorded from there in profusion during the Eocene, including such basically boreotropical genera as *Magnolia*, *Hypserpa*, *Tinomiscium*, *Meliosma*, *Phytocrene*, and *Mastixia*. A second route could have been via a North Atlantic land connection, which would probably have been at a lower paleolatitude than the Beringian connection (*cf.* McKenna, 1975). Paleobotanical evidence for this route is, however, lacking at the present time.

The floristic affinities of the boreotropical (including both megatherms and mesotherms) flora are very clearly Indomalayan in present distribution. The genera still extant include numerous Menispermaceae and Icacinaceae that are today restricted to this geographic area. Some of the more characteristic extinct genera are members of families such as Mastixiaceae or the tribe Phytocreneae of Icacinaceae, again groups now Indomalayan (Chandler, 1964). Thus, much of the present Indomalayan flora can be thought of as a relict of this Paleogene

boreotropical flora. This also means that even though a particular genus is now restricted to and diverse in Indomalaya, it did not necessarily originate in that region; clearly, the genus could have originated in North America or northern Eurasia, that is, in any of the areas formerly occupied by the boreotropical flora (see below).

Leopold & MacGinitie (1972) indicate that during the Paleogene the floristic affinities of the Rocky Mountain region changed from a dominantly paleotropical to a dominantly neotropical aspect. I suggest that the "neotropical" aspect is not austrotropical; the "neotropical" aspect is rather the result of the evolutionary trends in basically boreotropical groups, that is, the mesothermal boreotropical groups that have survived in North America will naturally become gradually more similar to the survivors in North America than to the survivors of the same groups in Asia.

The geographic extent of the boreotropical flora during the Eocene was variable. During warm intervals, this flora certainly extended to well beyond 50° N. in Europe, that being the most northern occurrence of Eocene plant-bearing deposits on that continent. In western North America, the most northerly Eocene deposits at a paleolatitude of at least 65° N. are clearly boreotropical (Wolfe, 1972). In eastern Asia, the picture is less clear, because the described Eocene assemblages all belong to the late Eocene cool interval; Tanai, however, has reported (oral communication, 1974) that in gross aspects, the as yet undescribed middle Eocene floras from Hokkaido are similar to those of Alaska and Washington. What this indicates, of course, is a similar physiognomy and megathermal climate, but the floristic aspects are still not certainly known.

The Paleogene pollen sequence from Borneo has been interpreted as being similar to the sequences from Nigeria and northern South America, but analysis of the Borneo material does not substantiate such a similarity. As noted previously, the Bornean material from the Upper Cretaceous contains the characteristic northern hemisphere *Aquilapollenites* and, as well, lacks the southern hemisphere true proteaceous pollen. Several of the Bornean pollen types, *e.g.*, *Nypa*, *Anacalosa* type, Rhizophoraceae, and Moraceae, are indeed found in the Paleogene of Africa and South America, but such types are also known in the boreotropical realm during the Paleogene. Some of the more characteristic African and/or South American Paleogene pollen types, *e.g.*, *Ctenolophon*, in fact do not appear in the Bornean succession until the Neogene, but the Bornean Oligocene contains the clearly boreal *Alnus* (Muller, 1966). Such data suggest that in the Paleogene, as in the Cretaceous, the Bornean assemblages represent the southern part of the boreotropical kingdom and that probably, as Reid & Chandler (1933) long ago surmised, the northern shores of Tethys supported a similar flora from Indomalaya northwest to western Europe.

The floristic composition of the Paleogene vegetation of southeastern North America is not well known. Despite the determinations published in an extensive series of papers by E. W. Berry (*e.g.*, 1930), more recent work by Dilcher and his colleagues (*e.g.*, Dilcher & Dolph, 1970; Dilcher, 1973) has demonstrated that most of Berry's determinations were rather fanciful. That extreme caution should be

exercised in accepting any of Berry's determinations is also indicated by the names he applied to foliage that has the cross-hatched petiolules characteristic of Leguminosae and Connaraceae. Such leguminaceous leaflets Berry called *Simaruba*, *Ficus*, *Sapindus*, *Mimusops*, *Banisteria*, *Carapa*, and *Myrcia*.

As yet, no exclusively South American or South American and African genus has been validly determined in the southeastern United States Paleogene. Elements such as *Oreomunnea*, *Engelhardia*, *Paraengelhardtia*, *Populus*, and aff. *Dendropanax*, are clearly Northern Hemisphere in origin. As might be expected, the flora also includes some pantropical elements, for example, *Cochlospermum* and *Memecylon* (Wolfe, unpublished data). The only possible austrotropical element is *Philodendron* (Dilcher, 1973).

During some parts of the Eocene, the southeastern United States had a dry tropical climate. The Claiborne assemblages, for example, have a consistently high representation of entire-margined leaf-species (80% or more), which probably indicates tropical temperatures. The leaves, however, typically lack drip-tips and the majority of the species are microphyllous; additionally, the leaf type associated in many instances with lianas (cordate-based and palmately veined) is uncommon. Therefore, while the climate was tropical, these other foliar characters indicate some deficiency of precipitation.

Whether the dry boreotropical flora of the southeastern United States contributed to the present dry tropical flora of the Caribbean has not been certainly determined. If, however, some of the Antillean region was land during the Eocene, it would appear probable that the flora of such islands would be closely allied to the flora of the southeastern United States. Following the Oligocene deterioration and the elimination of most megatherms from the continental area, some megatherms would surely have survived in the Antillean region. Thus, the present flora of the Antilles may well be derived from two distinct sources: the dry boreotropical Eocene flora and the lineages of austrotropical affinities that adapted to drying conditions in northern South America during the Neogene (Germeraad *et al.*, 1968: 271–272). Clearly, however, further work is needed to establish which source any particular Caribbean lineage had.

During the Paleogene, the boreotropical flora (in at least the humid areas occupied) had a considerably greater uniformity than did the floras of Africa and South America at that time. This interpretation is based, in part, on the many genera—both extinct and extant—that are known from the Paleogene of both Oregon and England (Chandler, 1964: 58–59). Considering the floristic differences between these regions during the Late Cretaceous, the Paleogene similarities almost certainly represent the establishment of direct migrational routes between the two regions. That such a route existed is also strongly indicated by similarities in the earlier Paleogene mammalian faunas of both regions (McKenna, 1975). Interestingly, although McKenna indicates that the direct European-North American mammalian migrations ended at the end of the early Eocene (ca. 49 m.y.), the floristic similarities endured through the early Oligocene (ca. 34 m.y.), which is the age of the Clarno fruit and seed flora (Evernden & James, 1964). In other words, floristic similarities at the generic level were still strong some 15 million years following the last direct migrational path.

BOREOTROPICAL-AUSTROTROPICAL RELATIONSHIPS

Dispersal of some groups was apparently easy during the Paleogene. An example of one such group is that represented by the olacaceous pollen *Anacolosidites* (this type of pollen characterizes the extant *Anacolosa, Cathedra,* and *Ptychopetalum*). According to Germeraad *et al.* (1968), *Anacolosidites* first appears in the Paleocene of Australia, Borneo, Eurasia, and Africa; the only time-lag in the appearance of *Anacolosidites* is in South America, where this pollen type does not appear until the Paleocene-Eocene transition.

As in the case of Bombacaceae cited previously, Menispermaceae (and conceivably Lardizabalaceae) strongly indicate that some floristic interchange occurred between North and South America during the Late Cretaceous and Paleogene, despite the apparent wide geographic separation of the two continents. Representing the same type of long distance dispersal (possibly aided by now-disappeared islands) is section *Lorenzanea* of *Meliosma* and the allied genus *Ophiocaryon.* Certainly *Meliosma* is a boreotropical contribution to the lowland rain forest of South America. Van Buesekom (1972) has strongly suggested that an Eocene species from California is close to the Amazonian *M. sellowii.* Except for the occurrence of *Philodendron* in the Eocene of Tennessee (Dilcher, 1973), I know of no contributions of South American groups to the North American Paleogene flora, but at least a few such contributions are to be expected.

Menispermaceae appear to be a family of boreotropical origin, but one that that has successfully invaded the austrotropical region more than once and from more than one direction. In Cocculeae, for example, the North American-Indomalayan *Cocculus* extends into Africa and thence to South America in the form of the monotypic *Ungulipetalum.* All the less advanced genera of this tribe are basically Indomalayan. In contrast, the Anomospermeae and Hyperbaenae, which are endemic to the neotropics, probably represent one or two dispersals from the boreotropical realm via North America; neither tribe has close relatives in Africa or Australia. Tinosporeae are pantropical, but the less advanced members are Indomalayan (Diels, 1910), except for *Calycocarpum* in the southeastern United States; the occurrences of this now mesothermal genus in the Paleogene Clarno flora of Oregon and London Clay flora of England (Chandler, 1964) rather clearly indicate that the Paleogene members were, at least in part, megatherms. One group of genera of Tinosporeae is today African (but one—*Jateorhiza*—is known from the London Clay), and represents one or more dispersals between Eurasia and Africa. Another group of genera is South American, but the only known fossil allied to this group is *Odontocaryoidea* from the Paleogene of Oregon (Scott, 1954, 1956), thus suggesting yet another dispersal of the family from North into South America. Menispermaceae today display no patterns strongly linking the Southern Hemisphere continents, in contrast to the numerous patterns—particularly in the Paleogene—that link the Northern Hemisphere continents. To emphasize this last point, it is highly significant that the same genera of Fibraureae, Tinosporeae, and Cocculeae, are known in both the London Clay and Clarno floras.

The close relationship of the European and African plates during the Paleogene conceivably gave rise to some floristic interchange between the two continents, but

available paleobotanical evidence indicates that such interchange was negligible. The London Clay flora (Chandler, 1964), for example, contains only two dicotyledonous genera of possible African derivation: *Jateorhiza* (Menispermaceae; 2 spp. tropical Africa) and *Oncoba* (Flacourtiaceae; 5 spp. tropical Africa). This possible African element is no larger than the Australasian element, which is composed of *Hibbertia* (Dilleniaceae; 100 spp. Madagascar, New Guinea, Australia, New Caledonia) and *Leucopogon* (Epacridaceae; 150 spp. Malaysia, Australia, New Caledonia). Some London Clay genera that are today both African and Indomalayan may, of course, have originated in Africa and spread to Eurasia during the Paleogene, but there is no available evidence that would indicate such a pattern. One point that deserves emphasis is that, although the African and Eurasian plates could have been adjoining one another, the epicontinental seaways may have been sufficiently wide to have inhibited interchange of land floras—a situation, as was pointed out above, that prevailed in the Cretaceous on the North American plate.

Had there been considerable floristic interchange between Africa and Eurasia during the Late Cretaceous and Paleogene, it would be expected that at least several groups would display disjunctions between the montane flora of Africa and the temperate lowland or montane flora of Eurasia. That is, the floristic disjunctions between the microthermal vegetation of the eastern United States/Upland Mexico and eastern Asia/Himalayas is primarily the result of the participation of such disjunct lineages during the Paleogene in lowland megathermal to mesothermal vegetation throughout the Northern Hemisphere and the subsequent adaptation of such lineages to microthermal climates in both Eurasia and North America (Wolfe, 1969*a*, 1972). A similar pattern would be expected in microthermal vegetation of Africa and Eurasia if the megathermal vegetation of the two continents could have been readily exchanged. Even more significant is the fact that the generic similarity of the mesothermal vegetation of Africa and Eurasia is extremely low. Genera such as *Meliosma*, *Magnolia*, *Talauma*, *Schima*, *Eurya*, *Liquidambar*, *Persea*, and *Quercus* are common in the mesothermal forests of Asia (Wang, 1961) and are also found in analogous forests in North America. Such genera are basically boreotropical derivatives. No such similarity is found between the mesothermal forests of Africa and Eurasia, and I conclude that this is the result of the lack of contact between the African and Eurasian floras during the Paleogene.

Not until the Neogene does there appear to have been significant floristic interchange between the boreotropical and austrotropical floras. This interchange has been discussed elsewhere (*e.g.*, Lakhanpal, 1970; Raven & Axelrod, 1972) in regard to the paleotropical region. As to which groups entered Africa from Eurasia and which groups had the reverse pattern, the fossil record is, unfortunately, not totally revealing. Neobotanical studies are in this instance of some value. For example, Kanis (1967) suggests that at least some genera of the tribe Ochneae of Ochnaceae entered the Eurasian region from Africa. The monogeneric Ctenolophonaceae, based on their fossil occurrences, almost certainly migrated into the Indomalayan area in the Neogene and have Paleogene occurrences in Africa (Germeraad *et al.*, 1968). Dipterocarpaceae have Paleogene records in the

boreotropical region (Rasky, 1956; Wolfe, 1972), but are unknown in Africa until the Neogene (Lakhanpal, 1970). More information is needed, however, in regard to most now paleotropical groups.

No analogous union of the austrotropical and boreotropical floras occurred in the neotropical region, however, and this phenomenon deserves further consideration.

Following the Oligocene, the boreotropical vegetation became highly restricted areally. Indeed, no megathermal vegetation is known in the Northern Hemisphere during the Neogene in areas that do not now support megathermal vegetation, which is now restricted to areas equatorward of latitude 20° to 25° N. Possibly, megathermal vegetation was even more restricted areally than now; areas such as lowland Taiwan, which is currently occupied by a megathermal rain forest (Li, 1963; Wang, 1961), were occupied by the mesothermal sclerophyllous "oak-laurel" vegetation during the early Miocene (Chaney & Chuang, 1967). I have suggested previously (Wolfe, 1971) that other paleobotanical data can be interpreted in the framework of lower latitudes having warmed during the Neogene.

Some of the boreotropical lineages may have, in fact, become extinct in the northern neotropical region during the Neogene. Langenheim *et al.* (1967), for example, record abundant juglandaceous pollen of the *Engelhardia* type (this includes *Engelhardia*, *Oreomunnea*, and *Alfaroa*) from rocks that represent lagoonal deposits in Chiapas. Langenheim *et al.* (1967) suggested that either the pollen represents an extinct, tropical lowland member of Juglandaceae or extant American genera that produce this pollen type and that are upland today had considerably different tolerances during the latest Oligocene or earliest Miocene than today. A third suggestion to explain this Chiapas occurrence is that, as in eastern Asia, mean annual temperature has increased during the Neogene, that is, *Oreomunnea* and/or *Alfaroa* have not significantly changed their tolerances.

If the third alternative just proposed is accepted as valid, then I suggest that the boreotropical affinities of the montane vegetation of Central America and the austrotropical affinities of the lowland vegetation of the same area become readily understandable. As noted earlier, at latitude 25° N. in Taiwan, a mesothermal climate prevailed during the early Miocene in a now megathermal climatic area. If an analogous situation occurred in North America following the Oligocene deterioration, the potential area of occupation by megathermal vegetation would have been extremely limited to a narrow strip at the southernmost edge of the North American plate. Such a limited area could hardly have supported the diversity previously known in the North American megathermal boreotropical vegetation. On the other hand, the mesothermal boreotropical vegetation would still have occupied considerable areas of the southern United States, perhaps extending even farther north (*cf.* MacGinitie, 1962, for a late Miocene occurrence in Nebraska of mesothermal elements). Thus, the megathermal boreotropical elements would have been limited in number but the mesothermal boreotropical elements still would have been diverse when the North and South American plates merged in the later Neogene. The rising mountains of Central America offered a ready area of occupation for the

boreotropical mesothermal elements, some of which (*Alnus*, *Juglans*) penetrated into South America (Graham, 1973).

In this connection, it is significant that the element in the Rocky Mountain Paleogene floras considered by Leopold & MacGinitie (1972) to be of neotropical affinities is now primarily found in the mesothermal areas of Central America. It is this area to which the North American part of the boreotropical flora is now largely restricted. Had the megathermal part of the American boreotropical flora not become largely extinct (except for some of the possible survivors in the Caribbean region), there would today be less of a distinction between the paleotropical and neotropical floras, that is, there would have been a merging of boreotropical with austrotropical megathermal elements in the New World analogous to the situation in the Old World.

The Neogene

The biogeography of many Northern Hemisphere regions during the Neogene (or following the Oligocene deterioration) is much better known than for the Paleogene. This is particularly true for areas poleward from 35°. In areas in which Neogene lineages can be traced back into the Paleogene, generally the lineages had been members of the broadleaved evergreen boreotropical vegetation, or of microthermal vegetation that had been present in upland areas. That is, many of the lineages had adapted at various times during the Paleogene to upland microthermal climates, a phenomenon suggested by Grubov & Federov (*e.g.*, 1964). In other instances, some lineages remained part of dominantly broadleaved evergreen vegetation until the occurrence of the Oligocene climatic deterioration. In yet other instances, lineages gradually adapted from mesothermal to microthermal climates following the deterioration (Wolfe, 1969*a*, 1972).

Although various "floristic elements" have been proposed for species occurring in, for example, the Neogene floras of western North America, the usefulness of recognizing such "elements" is uncertain. The "East Asian" and "East American" elements simply represent those lineages that have become extinct in western North America but whose putatively closest related lineages have survived in these other respective areas. Even if species in such elements are properly placed therein[2], the only information to be gained is that sometime in the past the extinct lineage and the extant lineage had a common ancestor; no information is gained concerning where or when the divergence occurred. Indeed, it is possible in an instance such as that of *Pterocarya* (s.l.), that an extinct west American lineage could be most closely related to another lineage that has become extinct in eastern North America, where pollen of the *Pterocarya/Cyclocarya* type is known from at least the Oligocene (Traverse, 1955) through the Pliocene (Wolfe, unpublished data). That is, the west American Neogene species of *Pterocarya* could conceivably indicate a strong floristic relationship with eastern North America rather

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[2] Chaney (1959), for example, relates the extinct west American *Quercus simulata* to the extant east Asian *Q.* (*Cyclobalanus*) *myrsinaefolia*, whereas I (1964) consider a more likely relationship to be with (although not ancestral to) the extant west American *Q.* (*Protobalanus*) *chrysolepis*.

than with eastern Asia and the Caucasus, where the sole survivors of the genus occur.

In many respects, the various "floristic elements" currently recognized may represent little more than ecologic convergences. Most of the genera concerned have not been thoroughly studied in the fossil record to determine whether the foliar similarities that supposedly link a fossil species with a particular extant species are of phyletic (and hence floristic) value. In an example discussed later, a species of *Mahonia* from the Miocene of Spain was thought to be related to the west American species of this genus (Amor, 1955). Although in gross morphology some similarities do exist, the fact that the Spanish leaflet is apparently palmately veined (characteristic of the Group Orientales of *Mahonia*) and that the putative relatives in western North America are all pinnately veined (characteristic of the Group Occidentales) indicates that the Spanish occurrence cannot be used to infer a floristic relationship between Spain and western North America during the Miocene.

The salient feature of Neogene microthermal vegetation is, however, that the flora of a given area appears to be largely derived from the preceding flora in that area (MacGinitie, 1962). That is, most lineages of the Neogene at middle to northern latitudes appear to have already been present in the Paleogene in the same area. Little floristic interchange, at least in regard to the ligneous flora, took place between, for example, Eurasia and North America (Wolfe & Leopold, 1967; Wolfe & Tanai, in press). There are, of course, some notable exceptions to this generality, particularly in the instances of Betulaceae and Salicaceae, both families undergoing considerable geographic expansion and specific diversification during the Neogene.

The Beringian area, which functioned as a major floristic pathway between North America and Eurasia during the Paleogene, did not serve as a major pathway for interchange between the broadleaved deciduous forests at middle latitudes of North America and Asia during the Neogene. This is true despite the fact that broadleaved deciduous forest extended in a continuous belt around the Northern Pacific as late as the middle Miocene. Although the middle Miocene flora of the Beringian region contains many species that also occur in Japan and many species that also occur in the Pacific Northwest, few species attained a distribution from the Pacific Northwest to Japan or vice versa (Wolfe & Tanai, in press). Thus, the floristic relationships in the later Cenozoic ligneous plants of the middle and high latitudes of the Northern Hemisphere largely (but not entirely) reflect Paleogene patterns. Van Steenis (1962) validly theorized that the distributional patterns of many now dominantly microthermal genera were bound up with the distributional patterns of mesothermal and megathermal genera.

There is no paleobotanical evidence that the floristic relationships between the dry floras of the Northern Hemisphere region are the result of interchange via low to middle latitude dry corridors. Although I have suggested that during the Eocene the southeastern United States was occupied by a dry tropical forest, it is clear that western Europe was occupied by a wet tropical forest, as was the southwestern United States. That is, during the Eocene there was no dry belt extending from the southwestern United States across into the Mediterranean

region. Indeed, I have shown that some of the so-called "Madro-Tertiary" dry elements were part of humid to mesic forests during the Oligocene and Neogene (Wolfe, 1964, 1969*b*), and the presence of a genus such as *Arbutus* in both western North America and Asia Minor in all probability is a reflection of a more widespread distribution of the genus in humid to mesic broadleaved and coniferous forests of the Paleogene. Axelrod (1966) has, in fact, recorded *Arbutus* from an Eocene flora, for which he inferred a microthermal climate with abundant precipitation well distributed throughout the year.

The berberidaceous *Mahonia* exemplifies in a slightly different manner how a distribution such as that of *Arbutus* could have been developed. One group (Occidentales) of *Mahonia* is centered in western North America and has been considered to be a "Madro-Tertiary" group (Axelrod, 1958), although the earliest record of this type of *Mahonia* is in mesic coniferous forest (Axelrod, 1966; Schorn, 1966). The Group Occidentales has, however, displayed in the Neogene a definite tendency to adapt to and diversify in subhumid to xeric environments (Schorn, 1966). The Group Orientales has an extensive Tertiary record in western North America, and is represented by both mesic and subhumid species; the bulk of this group, however, is now found in the humid to mesic forests of eastern Asia (arriving there by at least the early Miocene; Tanai, 1972). The Orientales, however, also expanded into Europe, where Neogene records include that from Hungary (Andreansky, 1959). Significantly, however, at least one lineage of the Group Orientales adapted to subhumid conditions in the Mediterranean region and has been recorded from the Neogene of Spain (Amor, 1955). *Mahonia*, however, subsequently became extinct in the Mediterranean region.

Yet another and possibly related distribution pattern is that of *Platanus*, which has some mesic species (*e.g.*, in the eastern United States) but could be cited as a floristic link between the dry vegetation of the Near East and southwestern North America. In fact, *Platanus* had a wide distribution in Paleogene (if not Cretaceous) broadleaved evergreen forests and persisted in broadleaved deciduous forests of eastern Asia through the Miocene (Tanai, 1972). In view of such distribution patterns, I suggest that there is no necessity to postulate that the current, rather meager, floristic similarities between dry areas of the Northern Hemisphere reflect a former continuity of dry habitats.

I emphasize, however, that this discussion has involved the ligneous flora. Little is known of the historical biogeography of the major herbaceous groups. A family such as Compositae appeared almost simultaneously on all continents near the Paleogene-Neogene boundary (Muller, 1970), in both tropical and extratropical regions. The patterns in such families are reflections of later Cenozoic phenomena, but at this time paleobotany has little to contribute regarding the distributional patterns of many of these advanced families.

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EVOLUTION AND BIOGEOGRAPHY OF MADREAN-TETHYAN SCLEROPHYLL VEGETATION[1]

Daniel I. Axelrod[2]

Abstract

Broadleaved evergreen sclerophyllous taxa occupied a subhumid belt across much of North America-Eurasia by the middle Eocene. They originated from alliances in older laurophyllous forests that adapted to spreading dry climate. Since the continued trend to aridity finally restricted sclerophyllous vegetation to subhumid areas separated by drier tracts, it now occurs in areas with summer rain as well as in summer-dry mediterranean climates. Taxa of chaparral and macchia habit are common undershrubs in sclerophyll woodlands, to which they are seral. Shrublands spread only recently, though the adaptive structural features of the taxa are ancient and probably not pyrogenic.

The history of Madrean-Tethyan sclerophyll vegetation illuminates three biogeographic problems. *First*, related taxa that link the Mediterranean-California areas are part of the larger problem of ties between these areas and those of summer rainfall, of taxa now in summer-rain areas that were in presently summer-dry areas into the early Pleistocene, and of the more numerous taxa that linked sclerophyllous vegetation of the Madrean-Tethyan regions during the Tertiary. The ties between summer-dry and summer-wet areas are relicts of the Neogene; taxa now in mediterranean-climate areas adapted functionally to these new climates during the Pleistocene; and most trans-Atlantic links owe to migration across a narrower ocean with more numerous islands, to a broader zone of subhumid climate, and to a more easterly trending Appalachian axis with numerous dry edaphic sites. *Second*, by the mid-Oligocene spreading dry climate had confined a formerly continuous temperate rainforest to southern Mexico, the West coast and the Appalachian area. Winter cold and summer drought exterminated it in the West, whereas in the East winter cold eliminated most evergreen dicots, leaving a dominantly deciduous hardwood forest there. The temperate "Appalachian disjuncts" in southern Mexico are therefore ancient, and did not migrate south to enter a forest previously without deciduous hardwoods, as others maintain. *Third*, the Canarian laurel forest derived its taxa from those in laurophyllous forests that covered northern Africa into the middle Miocene, not by southward migration from southern Europe in the Pliocene. Since many shrubs in the surviving laurel forest also contribute to macchia on bordering slopes, the ancient origin of their typical adaptive structural features is clearly implied.

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[1] Acknowledgments.—My current interest in this problem commenced in 1971, with my first glimpse of Mediterranean sclerophyllous vegetation, composed of *Arbutus*, *Ilex*, *Laurus*, *Pistacia*, *Phillyrea*, *Pinus brutia*, *Quercus* and *Rhus*. This was not a sunny, summer-dry Spain, but on the Black Sea coast near Inebolu, northern Turkey, where there is considerable rain during the summer months. There the sclerophyllous belt is replaced upslope at altitudes near 150 to 200m by a mixed deciduous hardwood forest composed of *Acer*, *Carpinus*, *Castanea*, *Corylus*, *Cotinus*, *Fagus*, *Juglans*, *Pinus nigra*, *Quercus* (deciduous), *Rubus* and *Sorbus*. The ecotone simulates the general composition of numerous late Tertiary floras of the Mediterranean region, as well as those in the western United States where members of sclerophyllous Madrean vegetation were also in ecotone with deciduous hardwood-conifer forests of Arcto-Tertiary alliance, though in each area the Neogene floras are far more diverse than the living.

To gather additional data for an analysis of the history and paleoecological relations of sclerophyllous vegetation, the U. S. National Science Foundation provided a grant (GB-37533) to visit other areas in the Mediterranean region. Funds from the Committee on Research, University of California, Davis, made it possible to study related sclerophyllous vegetation in northern Mexico and the southwestern United States.

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Sclerophyllous evergreen woodland and chaparral or macchia vegetation now inhabit discontinuous areas of subhumid climate across North America and Eurasia. They are remnants of an older sclerophyllous flora that appears to have originated from alliances in subtropical laurophyllous forests that evolved in response to the expansion of a new adaptive zone—dry climate. In North America, forerunners of modern sclerophyllous taxa appear in the middle Eocene, and their derivatives migrated widely as dry climate spread (Axelrod, 1958, 1967*c*, 1973). This sclerophyllous vegetation was captioned the Madro-Tertiary Geoflora because remnants of it survive in the Sierra Madre of northern Mexico and related ranges to the north, and because its taxa appear to have originated over this region. It occupied a position between Tropical-Tertiary and Arcto-Tertiary forests throughout its history, and in the ecotones with them it regularly includes taxa from these dissimilar environments.

Evergreen sclerophyllous vegetation has had a similar history in Eurasia, to judge from the brief analyses presented by Andreánszky (1962*a*, 1962*b*) and Takhtajan (1969). Its species were derived from alliances in older laurophyllous forests that adapted to dry climate that stretched across the Tethyan region of southern Eurasia by the later Eocene. As Andreánszky and Takhtajan note, it was situated between the Turgayan (Arcto-Tertiary) forests of mixed deciduous hardwoods and conifers that thrived under ample rainfall and mild temperate climate, and the Poltavian (Tropical-Tertiary) evergreen forests that were adapted to moist, subtropical and tropical conditions. Andreánszky felt the sclerophyllous flora had originated under dry climate in the Spain-Morocco region, and termed it a "Xero-Atlantic" element. However, Takhtajan (1969) noted that sclerophyllous vegetation was widespread across lands marginal to the Tethys Sea, and captioned it Tertiary-Tethyan vegetation.

The broadleaved sclerophyllous evergreen vegetation of the Madrean-Tethyan regions is similar in physiognomy and shares a number of related taxa. These relations have been considered by others, but chiefly in the context of affinities between the evergreen sclerophyllous floras of the Mediterranean basin and California which survive under mediterranean climate (Stebbins & Day, 1967; Walter, 1968; Raven, 1973). Among the alliances in common are species of *Arbutus*, *Cercis*, *Cupressus*, *Juniperus*, *Pinus* (closed-cone), *Platanus*, *Quercus* (evergreen), *Prunus* (*Laurocerasus*, *Emplectocladus*), *Rhus* (*Schmaltzia*), *Rhamnus*, *Staphylea* and *Styrax*. As to where and when the ties were established, some (*i.e.*, Engler, 1904, 1914) infer migration via subhumid climate around the north Atlantic; others (Stebbins & Day, 1967) suggest Miocene dry tracts in the lee of mountains along a Beringian route. Either route seems unlikely because (a) sclerophyllous taxa have not been recorded there, (b) moist temperate Arcto-Tertiary forests inhabited the region, (c) mountains of sufficient altitude to provide dry tracts were not yet elevated, and (d) xeric sclerophylls require short days, warm temperate to subtropical temperatures, and limited (subhumid) rainfall, a combination of conditions that can not occur at high latitudes. Engler (1904) also considered the possibility that ancient, now-sunken, Tertiary continental land bridges may account for the links between areas of mediterranean climate, and also between taxa of the desert and thorn scrub vegetation on opposite

sides of the Atlantic. Not only is there no geologic or geophysical evidence of low density (2.8) sialic land bridges in the denser (3.2) simatic basement of the Atlantic basin, but mediterranean climate is much younger than the sclerophylls because it only appeared after the early glacials. Meusel (1969) suggested the present Mediterranean-Californian disjuncts are the result either of parallel differentiation of holarctic or amphitropical taxa under similar climate, or of long-distance dispersal from one center to the other.

The presence of related taxa in the now widely separated mediterranean climates of North America and Eurasia becomes understandable when we note that on each landmass species that contribute to broadleaved evergreen sclerophyllous vegetation are not confined to areas of summer-dry, mediterranean climate (Axelrod, 1973). Many of them, or closely related ones, are also in subhumid regions of summer rainfall, as in Arizona-New Mexico or Nuevo León in southern North America, or in northern Turkey, Iran (Caspian shore), and northwestern India-Baluchistan. The fossil record shows that by the middle Tertiary essentially continuous, sclerophyllous vegetation belts covered each continent at low–middle latitudes where they thrived under subhumid climates with mild temperature and moderate rainfall in the warm season. Late in the Tertiary, decreasing temperature and reduced rainfall restricted sclerophyllous vegetation at the expense of spreading grassland, steppe and desert climates. The present discontinuous areas of sclerophyllous vegetation are therefore relict, and one of them occupies a wholly new climate (mediterranean) that seems to have appeared after the first glacial (Axelrod, 1966, 1973).

New evidence regarding the origin of sclerophyllous vegetation and the evolution of the adaptive characters of its taxa is considered here. A more complete explanation (Axelrod, 1971, 1972) of the present-day links between taxa now in the derived Madrean-Tethyan sclerophyllous zones is also presented. Furthermore, since spreading dry climate affected vegetation zones marginal to the expanding Madrean-Tethyan belt, two of them are considered. These are the history of the so-called "Appalachian" disjuncts in the Mexican-Central American temperate rain (cloud) forests, and the history of the sclerophyllous, evergreen Canary Island laurel forest that now inhabits the volcanic western Canaries, surrounded by ocean and desert.

BROADLEAVED SCLEROPHYLL VEGETATION

My field studies in North America and southern Eurasia have been concerned with the sclerophyll zone, the relation between woodland and chaparral or macchia vegetation, and the nature of the ecotones to adjacent vegetation. The basic findings are summarized here in terms of the evidence they provide with respect to its origin. The literature is so extensive that only a few critical references are noted.

MADREAN PROVINCE

Evergreen sclerophyllous woodland and chaparral have been studied in the following areas.

California
Closed-cone pine forest and chaparral
Inverness at Tomales Bay; Monterey; Purisima Hills near Lompoc; Pecho Hills near San Luis Obispo; Santa Cruz Island.
Pinyon pine-juniper woodland and chaparral
Wrightwood, San Gabriel Mts.; Anza-Bautista Creek, San Jacinto Mts.; Rattlesnake Mt., San Bernardino Mts.; Frazier Mt. Park, Mt. Pinos; Rattlesnake Canyon, Cuyama Valley.
Digger pine woodland and chaparral
Throughout inner Coast Ranges and lower slopes, Sierra Nevada.
Englemann oak woodland and chaparral
Interior southern California, Pasadena to Campo.
Walnut-oak woodland
Coastal southern California, from Montecito south to Santa Ana River valley.
Baja California
Live oak woodland and chaparral
Sierra San Pedro Martir.
Closed-cone pine forest
W of San Vicente.
Arizona
Pinyon-juniper woodland and chaparral
Hualpai Mts., S of Kingman; Payson-Pine-Verde River; Highway 60 W of Miami; Highway 84 SW of Prescott; S slope, Catalina Mts.; Mescal Mts., S of Globe.
New Mexico
Oak-juniper woodland and chaparral
Highway 82 W of Cloudcroft; Highway 90 W of Kingston.
Eastern Mexico (Nuevo León to San Luis Potosí)
Pinyon pine-juniper woodland
Near Galaena, Nuevo León; near La Escondida, Nuevo León; W base of S Pena Nevada, Nuevo León.
Oak woodland and chaparral
Vic. Cerritos, San Luis Potosí; vic. Guadalcazar, San Luis Potosí.

It is amply clear that sclerophyllous vegetation inhabits regions other than the wet winter and dry summer climate that distinguishes the climate of California, and which is usually associated with its occurrence. Sclerophyllous vegetation is well developed across central Arizona and eastward into New Mexico and Texas, a region of subhumid climate with winter and summer precipitation. Chaparral and evergreen woodland also cover extensive areas on the western slopes of the Sierra Madre Oriental in eastern Mexico, from near Saltillo southward into San Luis Potosí, a region of summer rain and winter drought. Some species are common to two or three of these regions, or are represented there by paired-species (Table 1). These include taxa that contribute to chaparral, as well as to the pine-oak woodland that borders chaparral or is mixed with it.

TABLE 1. Some identical and closely related taxa in sclerophyllous vegetation in subhumid Madrean North America (* = fossil occurrence).

Taxa	California	SW United States	E Mexico
Arbutus	*menziesii*	—	*xalapensis*
Arctostaphylos	*pringlei*	*pringlei*	—
Arctostaphylos	*pungens* *(*prepungens*, Miocene)	*pungens*	*pungens*
Bumelia	*(*beaverana*, Miocene, Nevada)	*lanuginosa*	*lanuginosa*
Ceanothus	—	*fendleri*	*fendleri*
Ceanothus	*greggii*	*greggii*	*greggii*
Ceanothus	*insularis* *(Miocene)	—	*coeruleus*
Celtis	—	*iguanea*	*iguanea*
Celtis	*(Miocene)	*pallida*	*pallida*
Celtis	*reticulata* (very rare) *(Miocene & Pliocene)	*reticulata*	*reticulata*
Cercis	*occidentalis* *(*carsoniana*, Miocene, Nevada)	*occidentalis* (very rare)	—
Cercocarpus	*montanus* (= *betuloides*) *(*antiquus*, Miocene & Pliocene, California & Nevada)	*montanus*	—
Cercocarpus	*(*holmesii*, Miocene, Nevada)	*paucidentatus*	*paucidentatus*
Cercocarpus	*traskiae*	—	*mojadensis*
Comarostaphylos	*diversifolia*	—	many species
Cupressus	*forbesii*; other species *(*preforbesii*, Miocene & Pliocene)	*arizonica*	*arizonica*
Dioon	*(undescribed, Miocene)	*purpusii* (NW Sonora-Sinaloa)	*edule*
Dodonaea	*(*californica*, Miocene & Pliocene)	*angustifolia*	*angustifolia*
Erythrina	—	*flabelliformis*	*flabelliformis*
Fraxinus	*dipetala*	*dipetala* (very rare)	—

TABLE 1. (continued)

Taxa	California	SW United States	E Mexico
Fraxinus	*velutina* (S California only) *(*alcorni*, Miocene, Nevada)	*velutina*	*berlandieriana*
Fremontodendron	*californicum* *(Miocene, California)	*californicum* (very rare)	—
Garrya	*elliptica* *(*masoni*, Pliocene)	—	*ovata*
Garrya	*(*axelrodi*, Miocene, Nevada)	—	*ovata*
Garrya	*flavescens*	*flavescens*	—
Garrya	*wrightii*	*wrightii*	*wrightii*
Gaultheria	*shallon*	—	*hartwegiana*; many species
Ilex	*(*sonomensis*, Pliocene)	*brandegeei* (S Baja California)	—
Ilex	*(undescribed, Miocene)	—	*rubra* (W Mexico)
Juglans	*(Pliocene; Miocene, Nevada)	*rupestris-major*	*mollis*
Juniperus	*californica*	*monosperma*	*deppeana*; *mexicana*
Karwinskia	*(*californica*, Miocene & Pliocene)	—	*humboldtiana*
Mahonia	*fremontii* (rare)	*fremontii*	*fremontii*
Mahonia	*(Miocene, Nevada)	—	*gracilens*
Mahonia	—	*trifoliata*	*trifoliata*
Morus	—	*microphylla*	*microphylla*
Myrica	*(*mohavensis*, Miocene)	—	*mexicana*
Persea	*(*coalingensis*, Miocene & Pliocene)	—	*borbonia*; *podadenia*
Pinus	*monophylla*; *quadrifolia*	*edulis*	*cembroides*; *nelsoni*; *pinceana*
Platanus	*racemosa*	*wrightii*	—
Populus	*fremontii*	*fremontii*	*arizonica*

TABLE 1. (continued)

Taxa	California	SW United States	E Mexico
Populus	*(*sonorensis*, Miocene & Pliocene, S California)	*brandegeei* (S Baja California)	—
Prunus	*(Miocene, S California)	*virens*	*virens*
Quercus	*(*mohavensis*, Miocene)	—	*brandegeei* (Baja California); *fusiformis* (NE Mexico).
Quercus	*(undescribed, Miocene, S California)	*emoryi*	*emoryi*
Quercus	*chrysolepis* *(*hannibali*, Miocene & Pliocene)	*chrysolepis*	—
Quercus	*dunnii* (= *palmeri*) *(*pliopalmeri*, Miocene & Pliocene)	*dunnii*	—
Quercus	*engelmannii* *(Miocene & Pliocene)	*oblongifolia*	—
Quercus	*(*turneri*, Miocene)	*grisea*	*grisea* (*Zacatecas*)
Quercus	*turbinella* *(*dispersa*, Miocene, S California)	*turbinella*	—
Quercus	*(*orindensis*)	*vaseyana* (W Texas)	—
Quercus	*(undescribed, Miocene, S California)	—	*potosiana*
Quercus	*(*dayana*, Miocene, C & S California)	*fusiformis*	*virginiana* (on coastal plain)
Rhamnus	*californica* *(*precalifornica*, Miocene)	*californica*	species
Rhamnus	*ilicifolia* *(Miocene)	*ilicifolia*	—
Rhus	*(*sonorensis*, Miocene)	*virens*	*virens*
Rhus	*(*tehachapiensis*, Miocene)	*chondroloma*	—
Rhus	*(undescribed, Miocene)	*microphylla*	*microphylla*
Rhus	*trilobata*	*trilobata*	*trilobata*

TABLE 1. (continued)

Taxa	California	SW United States	E Mexico
Rhus (*Schmaltzia*)	*ovata* *(*preovata*, Miocene & Pliocene; Miocene, Nevada)	*ovata*	—
Ribes (*Grossularia*)	*quercetorum* *(*mehrtensis*, Pliocene)	*quercetorum*	—
Robinia	*(*californica*, Miocene & Pliocene)	*neomexicana*	—
Sabal	*(*miocenica*, Miocene & Pliocene, S California)	—	*mexicana*; *uresana*
Sageretia	*(Miocene, S California)	*wrightii*	*wrightii*
Salix	*lasiolepis*	*lasiolepis*	*lasiolepis*
Salix	*exigua*	*taxifolia*	*taxifolia*
Sapindus	*(*oklahomensis*, Pliocene)	*drummondii*	*drummondii*
Ungnadia	*(*clarkii*, Miocene)	*speciosa*	*speciosa*
Vauquelinia	(Oligocene, Nevada)	*californica*	*corymbosa*
Zizyphus	*(Miocene)	*obtusifolia*	*obtusifolia*

In all these areas evergreen oaks and nut-pines form a rich woodland that has numerous sclerophyllous shrubs and typically borders chaparral or grades into it. At lower, drier levels from Arizona to eastern Mexico, both give way to grassland, or to desert where grassland has been overgrazed. In California, drier sites below chaparral are covered with oak savanna, or with sage or grassland. At higher, moister and cooler levels in eastern Mexico pinyon pine-juniper-oak woodland is replaced by a low montane forest dominated by oaks, or by a rich mesic cloud forest (Muller, 1939; Rzedowski, 1966). In Arizona-New Mexico, chaparral alternates with sclerophyllous oak-madrone woodland or with pinyon-oak woodland, and all are replaced at higher moister levels by mixed conifer forest. Similar relations exist in California, where its taxa additionally contribute to the understory of closed-cone pine forest in the coastal strip. This community closely parallels in physiognomy, and somewhat in composition, the *Pinus halepensis-brutia-Quercus* woodland vegetation of the Mediterranean coastal strip.

The sclerophyllous taxa in the woodlands and brushlands that stretch from California to eastern Mexico are interrupted now by more arid climates that support grassland and desert vegetation. As deduced by Clements (1936), a wider distribution at times of moister climate accounts for similar taxa in the chaparral and woodland on opposite sides of the Mohave and Sonoran desert regions in

California and Arizona, a conclusion supported now by additional fossil evidence (Axelrod, 1958, 1973). During the Miocene sclerophyllous woodland with a rich understory of sclerophyllous evergreen shrubs inhabited the present Mohave-Sonoran region. This implies 20–25 inches precipitation distributed in summer and winter, and mild temperature as judged from *Persea*, *Lyonothamnus*, *Myrica*, *Laurocerasus* and *Clethra*. Since most of the Miocene species appear indistinguishable from those now living, the identical species on opposite sides of the desert are no younger. As for the paired-species that provide links across the region, isolation may account for the differences, though this problem can only be settled by a more complete fossil record. In any event, a Neogene continuum that stretched from northeastern Mexico to California has been segregated into climatic subregions since the early Quaternary, following which dry climates rapidly expanded in each of the successive interglacial ages.

TETHYAN PROVINCE

Areas of sclerophyllous oak-pine-olive woodland and laurel woodland with a rich understory of shrubs that regularly contribute to macchia on bordering slopes have been examined in the following areas.

Canary Islands
  Laurel forest and matorral
    La Palma; Tenerife; Gran Canary.
Morocco
  Argania-Tetraclinis woodland and macchia
    Agadir to Imouzzer; NE of Taroudant.
Spain
  Pinus halepensis-Quercus ilex-suber woodland and macchia
    Seacoast E of Barcelona; Malaga-Ronda-San Roque.
France
  Pinus halepensis woodland and macchia
    Maritime Alps, vic. Nice.
Turkey
  Pinus brutia woodland and macchia
    Alacam-Sinop-Inebolu, Black Sea Coast; Ismir-Mansia-Kusadasi; Marmaris-Fethiye-Mugla; Antalya-Akseki-Korkuteli-Dag.
Iran
  Sclerophyll woodland and macchia
    Caspian seacoast.

In this region, macchia and sclerophyllous woodland thrive where precipitation is chiefly in winter and where there is a severe summer drought (Spain-Morocco-SE Turkey-Israel). Rainfall amounts and characteristics of summer drought of coastal California are most nearly matched in the eastern Mediterranean (Lebanon, Israel). Summer drought is not as pronounced along the shores of the Mediterranean as in California, and is replaced by summer-rain regimes in the mountains close to the sea, as in the Iberian, Italian, Balkan, and Anatolian peninsulas. The coastal fringe of summer-dry climate broadens in the African sector of the

TABLE 2. Some sclerophyllous links across the Tethyan region. Data from Meusel & Schubert (1971); Kitamura (1964); Meher-Homji (1973).

Taxa	Mediterranean *(& Canarian)	Mts. of Iran-Afghanistan	NW Himalayas to Baluchistan
Celtis	*australis*	*caucasica*	*caucasica; australis*
Cotinus	*coggygria*	*coggygria*	*coggygria*
Cupressus	*sempervirens*	*sempervirens*	*torulosa*
Daphne	*oleoides*	*oleoides*	*cashmirana*
Hedera	*helix* *(var. *canariensis*)	*himalayica*	*himalayica*
Ilex	*colchica*; ?*balaerica* *(*platyphylla*; *canariensis*)	—	—
Juniperus	*phoenica*	—	—
Laurus	*nobilis* *(*canariensis*)	*nobilis* (to Iran)	—
Myrtus	*communis*	*communis*	*communis*
Nerium	**oleander*	*odorum*; *mascatine*	*odorum*
Olea	**europa*	*europa*	*ferrugina*
Persea	*(*indica*)	—	*indica*
Pinus	*(*canariensis*)	—	*roxburghii*
Pistacia	**lentiscus*; *mutica*; *terebinthus*	*mutica*	*integerrima*; *mutica*; *terebinthus*
Punica	*granatum*	*granatum*	*granatum*
Pyracantha	*coccinea*	*coccinea*	*crenulata*
Quercus	*ilex*	—	*baloot*
Rhamnus	*oleoides*; *(*glandulosa*) *catharticus*; other species	*catharticus*; other species	*catharticus*; other species
Rhus	**coriaria*	*coriaria*	? (in Turkestan)
Sageretia	*spinosa*	*spinosa*; *thea*	*brandethiana*; *thea*

Mediterranean, which is much drier than the European shore. It is also noteworthy that the severity of summer drought in the northern Mediterranean is alleviated by the regular occurrence of heavy rains into late spring (June) and they return suddenly in early autumn (October), thus reducing drought stress appreciably. On the north shore of Turkey, from near Zonguldak to Sansum, sclerophyll vegetation thrives under precipitation that is well distributed through the year, and with at least 1 to 2 inches during *each* summer month. Macchia and woodland extend discontinuously eastward, reappearing on the Caspian sea coast of northern Iran, and in the northwestern Himalayas (Meusel, 1971; Meusel & Schubert, 1969; Meher-Homji, 1973), where rainfall is chiefly in summer. The distribution of

sclerophyllous vegetation across Eurasia clearly parallels that in North America at similar latitudes, with taxa extending from areas with protracted summer drought (California-Spain) to those with ample summer rainfall (Nuevo León, N Turkey, Caspian seacoast). As in North America, some taxa range widely across southern Eurasia, though others are replaced by related species or varieties in regions of different subhumid climates. Representative taxa that are discontinuous across southern Eurasia are listed in Table 2.

The sclerophyllous shrubs that make up macchia commonly comingle with an evergreen (oak-laurel-olive) woodland that in many areas has been degraded by man's activities. At lower, drier levels or to the south in Africa, woodland-macchia gives way to desert grassland, or to steppe and desert in the drier colder interior of Turkey and Iran. At moister, cooler and higher levels in the Mediterranean basin, sclerophyll vegetation is replaced by a mixed conifer-hardwood forest of *Abies*, *Cedrus*, *Picea*, *Pinus*, *Acer*, *Betula*, *Carpinus*, *Castanea*, *Fagus*, *Quercus* (deciduous), *Tilia* and their common associates. In northern Turkey and Iran (Caspian shore) a narrow belt of sclerophyllous woodland quickly gives way to a mesophytic deciduous hardwood forest composed of *Acer*, *Alnus*, *Carpinus*, *Castanea*, *Diospyros*, *Fraxinus*, *Gleditsia*, *Juglans*, *Morus*, *Parrotia*, *Quercus*, *Ulmus* and *Zelkova*. In India, sclerophyll woodland is bordered by thorn scrub at lower warmer levels, and by mesic mixed deciduous hardwood forests at cooler, moister altitudes (Meusel, 1971; Meusel & Schubert, 1969; Meher-Homji, 1973).

As in North America, the areas of sclerophyllous woodland and macchia that stretch across southern Asia are isolated by more arid climates that support grassland, steppe or desert vegetation. During Neogene time, evergreen sclerophyllous vegetation covered southern Spain, France, Italy, Greece, Turkey, as well as areas farther east that are now too cold or dry for it. For example, the Sarmatian (16 m.y.) flora from Vale in Georgian USSR has 60-odd species (Chelidze, 1970), including a palm, *Ilex*, *Hedera*, *Laurus*, *Paliurus*, *Quercus*, *Sapindus* and *Zizyphus* that occupied warmer slopes bordering a mixed deciduous hardwood forest. Also, the early Pontian (~ 10–12 m.y.) Kodor River flora of 100-odd species from north of Kutaisi in Georgian USSR has numerous hemixerophytes, notably *Arbutus*, *Ceratonia*, *Chamerops*, *Cotinus*, *Hedera*, *Ilex*, *Laurocerasus*, *Laurus*, *Myrtus*, *Persea* and *Pistacia* that are similar to species in the Mediterranean woodland and macchia today (Kolakovskii, 1964). They inhabited warmer slopes bordering a rich deciduous-evergreen hardwood forest that had numerous taxa that now survive in eastern Asia (*Berchemia*, *Carya*, *Cinnamomum*, *Eucomia*, *Fortunearia*, *Magnolia* and *Sophora*) which indicate ample rainfall in summer.

Clearly, a broad ecotone existed at the general latitude of the northern Black-Mediterranean seas (~ Lat. 40°), with more numerous sclerophylls dominant to the south and with conifers and deciduous hardwoods of moist temperate requirements replacing them to the north (Szafer, 1946; Depape, 1928; Kutuzkina, 1974; Takhtajan, 1969). This closely parallels the distribution of similar vegetation in the western United States at this time (Axelrod, 1967*a*: fig. 1; 1968: fig. 7). The Tertiary sclerophyllous vegetation of the extended Mediterranean region, which may be captioned the Tethyan-Tertiary Geoflora, is clearly an eastern counterpart

of the Madro-Tertiary Geoflora of southeastern North America, as noted earlier by Andreánszky (1962*a*, 1962*b*), Takhtajan (1969), and Meusel (1969).

Inasmuch as sclerophyllous vegetation was more widely spread in the Miocene and earlier times in both southern Eurasia (Tethyan) and North America (Madrean), and since there are taxa now common to these provinces, the questions naturally arise as to (1) the factors that account for the origin of the taxa that characterize the zones, (2) the paleogeographic setting that provided a means for interchange between these now widely separated areas, and (3) the impact the history of sclerophyllous vegetation had on adjacent vegetation zones.

Origin

floristic sources

Forests of tropical to subtropical requirements covered low–middle latitudes of North America and Eurasia during the late Cretaceous and Paleocene (Chaney, 1947; Krystofovich, 1929, 1935; Takhtajan, 1969). They largely represent ancient oak-laurel-palm forests that lived under monsoonal climate, with precipitation concentrated in the warm season and with warm summers and frostless winters. In North America, they inhabited swampy (coal) basins and broad floodplains at or close to sea level, both in coastal regions (Alberhill and Goler floras, southern California; Ripley flora, Alabama; Midway-Indio floras, Texas-Alabama) and the interior (Vermejo-Raton floras, northeast New Mexico, Fruitland-Kirtland and Animas floras, northwest New Mexico; Coal Creek flora, central Arizona).

At this time, taxa of relatively xeric requirements largely inhabited drier, exposed slopes on distant hills away from the floodplains and swampy basins of high water-table, sites from which they could have contributed but little to the accumulating record. This inference is consistent with the occurrence of a few taxa with small (microphyll to nanophyll) sclerophyllous leaves in the Fruitland-Kirtland and Ripley floras of late (Maastrichtian) Cretaceous age. Furthermore, some of the alliances in the late Cretaceous and Paleocene appear to be the forerunners of those in the succeeding laurel-oak-palm forests of the Eocene (Axelrod, 1958: 451–452) including species of *Bumelia*, *Clethra*, *Colubrina*, *Dodonaea*, *Karwinskia*, *Pithecolobium*, *Platanus*, *Ficus*, *Persea*, *Quercus*, *Sabal*, *Thouinia* and *Zanthoxylum*. In addition, the Eocene "Wilcox" flora includes *Bumelia*, *Clethra*, *Dodonaea*, *Karwinskia*, *Pithecolobium* and several other woody legumes, *Thouinia*, *Vauquelinia* and *Zanthoxylum*.

Dry climates had expanded over the interior by the middle Eocene, and ancestors of the present xerophyllous taxa were making their appearance (Axelrod, 1939, 1950; Leopold & MacGinitie, 1972). Among the small trees and shrubs that contributed to woodland vegetation in the Middle Eocene Green River flora of the central Rocky Mountain region are *Bursera*, *Cardiospermum*, *Celtis*, *Caesalpinia* (and other woody legumes), *Mahonia*, *Ocotea*, *Persea*, *Pinus* (nut pine), *Platanus*, *Populus*, *Quercus*, *Rhus*, *Sapindus*, *Styrax*, *Swartzia*, *Thouinia* and *Vauquelinia* (Axelrod, 1958: 448; MacGinitie, 1969). By the Eo-Oligocene, as judged from the Florissant flora (Axelrod, 1958: 450; MacGinitie, 1953) more numerous taxa were present, notably species of *Bursera*, *Cardiospermum*,

Celtis, *Cercis*, *Cercocarpus*, *Colubrina*, *Conzattia*, *Cotinus*, *Daphne*, *Dodonaea*, *Euphorbia*, *Ephedra*, *Mahonia*, *Morus*, *Platanus*, *Populus*, *Prosopis*, *Ptelea*, *Rhus*, *Rhamnus*, *Robinia*, *Sapindus*, *Stipa*, *Thouinia*, *Trichilia*, *Vauquelinia* and *Zizyphus* (*Condalia*). They lived under mild, frostless climate with precipitation concentrated in the warm season. This is implied by paleogeographic relations (warm oceans, no ice caps, no major cordilleras, low continents) and by the taxa and their associates that occur today only in areas with summer rainfall.

Descendants of these alliances make up xerophyllous woodland and chaparral vegetation today. Furthermore, the same species or allied ones regularly contribute to mesic oak-laurel-palm forest, or to oak-pine or oak forests that border the drier sclerophyllous woodland and chaparral in Mexico and the southwestern United States today. This implies many of these sclerophylls were derived from taxa in subtropical evergreen forests that had inhabited the region, including species of:

Anacardiaceae
- *Rhus*
- *Schmaltzia*

Aquifoliaceae
- *Ilex*

Berberidaceae
- *Mahonia*

Ericaceae
- *Arbutus*
- *Arctostaphylos*
- *Comarostaphylos*
- *Gaultheria*
- *Vaccinium* (evergreen)

Fagaceae
- *Quercus*

Leguminosae
- *Bauhinia*
- *Sophora*

Myricaceae
- *Myrica*

Myrtaceae
- *Eugenia*
- *Psidium*

Oleaceae
- *Forestiera*

Rhamnaceae
- *Ceanothus*
- *Condalia*
- *Karwinskia*
- *Rhamnus*

Rosaceae
- *Cercocarpus*
- *Heteromeles*
- *Laurocerasus*
- *Prunus*
- *Vauquelinia*

Rutaceae
- *Choisya*
- *Helietta*

Styracaceae
- *Styrax*

Sapindaceae
- *Dodonaea*

Verbenaceae
- *Citharexylum*

Woodland with a rich understory of sclerophyllous shrubs had already occupied southeastern California by the Miocene, as shown by the composition of the Vasquez and Mint Canyon floras which have been displaced 150–175 miles northwest from their original areas in the Chocolate-Orocopia Mountains by movement along the San Andreas fault (Crowell, 1962; Ehlig & Ehlert, 1972). Included are members of a sclerophyllous woodland (*Arbutus*, *Lyonothamnus*, *Persea*, *Populus*, *Quercus*- 6 spp., palm, *Ilex* and *Thouinia*) and numerous shrubs (*Ceanothus*, *Cercocarpus*, *Fremontodendron*, *Prunus*, *Quercus*, *Rhus* and *Schmaltzia*) that may have formed local, seral brushlands on drier slopes with shallow

soil. Annual rainfall was near 20–25 inches as compared with scarcely 3 inches today. Temperatures were relatively moderate as judged from the *Laurocerasus*, *Lyonothamnus*, *Malosma*, *Persea* and others that are found chiefly in mild climates today. The absence of frost is indicated by these taxa, as well as by the numerous woody legumes, *Bursera*, *Cardiospermum*, *Celtis*, *Euphorbia*, *Randia* and others that contribute to thorn scrub. Sclerophyllous oak-laurel woodland and thorn scrub had already covered the south end of the Sierra Nevada by the middle Miocene (17 m.y.) as shown by the Tehachapi flora (Axelrod, 1939).

Although large Neogene floras are not now known from the area farther east, the continuity of sclerophyllous vegetation across the subhumid part of North America may be inferred from the present distribution of similar taxa in sclerophyllous oak woodland and chaparral in Arizona, New Mexico, west Texas and eastern Mexico. Hint of a former continuous zone is implied by a small early Pliocene pollen flora from west-central Arizona (Gray, 1960*a*) which resembles conifer-oak woodland and associated chaparral like that in central Arizona today, with *Quercus*, *Pinus*, *Juniperus-Cupressus*, *Juglans*, *Celtis*, *Agave* and others that imply continuity since then. The early Pliocene Clarendon flora of northern Texas includes seeds of manzanita and *Sabal* palm (Chaney & Elias, 1936: 12). Further, there are xerophyllous taxa in the Miocene of Nebraska (MacGinitie, 1962), implying they were more dominant in areas to the south. The transitional Oligo-Miocene Creede flora (27–28 m.y.) of Colorado has a rich juniper woodland and chaparral (*Cercocarpus* and *Peraphyllum*) which is consistent with the inference of widespread sclerophyllous woodland to the south. The continuity of sclerophyllous woodland was disrupted by spreading dry climates which enabled grassland, steppe and desert vegetation to displace it. Sclerophyllous vegetation was segregated into three major subhumid regions (California, Arizona to west Texas, northeast Mexico) following the Tertiary, and it is this that accounts for the east-west discontinuous distribution of the taxa today (Table 1). That these restrictions in range are very recent is apparent from the record in California which shows that taxa (*Persea*, *Magnolia* and *Sapindus*) that are now found far to the southeast in summer rain areas were in California into the early Pleistocene (Soboba flora; San Joaquin flora).

In southern Eurasia, taxa of sclerophyllous woodland-macchia alliances were also preceded by more mesic laurophyllous forests. In the late Cretaceous, the Tethyan region was characterized by evergreen trees and shrubs, representing numerous Lauraceae, evergreen Fagaceae and palms that thrived under warm temperate to more tropical climate southward. The Tethyan-Cretaceous sub-tropical flora inhabited the shores of the Tethys and its islands, reaching across southern Europe and into southwestern Asia. It no doubt extended farther east into southwestern China, for the entire region from North Africa to southwestern China was a dry belt, as shown by the occurrence there of saline (gypsum, salt) deposits and red beds (Strakhov, 1967: vol. 1, chap. 5).

As in North America, there was a rapid modernization of generic composition during the Paleogene. Whereas the affinities of many genera of the late Cretaceous are doubtful, numerous Eocene plants can be referred to modern genera, and Oligocene floras are made up primarily of living genera whose species show some

affinity with living ones. In the early Paleogene, the Tethyan region of North Africa was situated at lower latitudes (Phillips & Forsyth, 1972), dominated by tropical forest and savanna. Numerous fossil woods indicate evergreen alliances chiefly, as implied by records of Annonaceae, Combretaceae, Dipterocarpaceae, Ebenaceae, Euphorbiaceae, Fagaceae, Lauraceae, Leguminosae, Moraceae, Myrtaceae, Rutaceae, Sapindaceae, Sterculiaceae and Tamaricaceae (Aubréville, 1970). As noted by Takhtajan (1969: 183), the Tethyan-Tertiary region was characterized by subtropical forests composed of evergreen trees and shrubs. Leaf floras have taxa referred to *Cinnamomum*, *Laurus*, *Litsea*, *Neolitsea*, *Persea*, and with *Quercus*, *Lithocarpus* and *Castanopsis* in the Fagaceae. There were also numerous palms, notably the genera *Chamerops*, *Livistonia*, *Sabal* and *Trachycarpus* (Takhtajan, 1958). To the north, generally commencing at the latitude of Kazakhstan, subtropical forests graded into the Arcto-Tertiary forests composed of temperate deciduous hardwoods, conifers, and some broad-leaved evergreens (Makulbekov, 1972).

Markedly xerophyllous floras had appeared by the later Eocene and early Oligocene. The transitional Eo-Oligocene flora from Er Olian Duz, close to the Afghanistan border in southern Turkmenia, is markedly xerophytic (Korovin, 1932; Vasilevskaya, 1957), composed of various laurels, and taxa referred to *Rhus*, *Zizyphus* and others. As emphasized by Takhtajan (1969: 200), the floras in southern Kazakhstan are also xerophyllous, as shown by the narrow leaves and their coriaceous texture (Budantsev, 1957). The floras of the southern Urals are similar, with dicots represented by small, narrow, and revolute leaves with mostly a coriaceous texture, and referred to *Myrica*, *Quercus* and other evergreens (Uznadze-Dgebudze, 1948). Clearly, environmental conditions in the broad region from Spain eastward to central Asia were favorable for the origination of mediterranean-type taxa, some of which appear to be foreshadowed in these and other floras, as noted by Andreánszky (1962*a*). Among the taxa he lists are *Arbutus*, *Laurus*, *Persea*, *Tetraclinis*, *Quercus*, *Myrsine*, *Myrica*, *Rhamnus* and *Zizyphus*, all represented in the early Tertiary floras of central Europe (which was then situated further south), and in the Neogene of the Mediterranean region. They are microphyllous or stenophyllous with hard leaves and other xeric features. Captioned the "Xero-Atlantic" element by Andreánszky (1962*b*), he inferred it originated at low middle latitudes, probably in the area of Spain-Morocco. Their origin in response to spreading dry climate over southern Eurasia now seems demonstrated.

By Oligocene and early Miocene times, the lowlands of the Mediterranean region were clothed with a broad sclerophyll woodland composed of oaks, laurels, palms, olives and numerous sclerophyllous shrubs, as shown by the floras from eastern Spain (Cervera flora: Bataller & Depape, 1950; Depape & Brice, 1965), the Balearic Islands (Arenes & Depape, 1956), and central Italy (Sinigaglia flora: Massalongo & Scarabelli, 1859). As emphasized by Depape & Brice (1965), these floras are xerophyllous, and show scarcely any relation to the temperate deciduous hardwood forests that thrived to the north. Sclerophyllous vegetation extended far to the east, as demonstrated by the nature of the flora in the Caucasus region, in the ecotone with the Arcto-Tertiary Geoflora. Also, the distribution of modern

taxa (*Punica*, *Nerium*, *Olea*, etc.) discontinuously eastward into the northwestern Himalayas and southwest China parallels the discontinuous distribution of the xerophyllous vegetation in the western United States-northern Mexico and, like it, implies a Neogene connection via subhumid climate across regions that are presently too dry or too cold for them.

Floristic relations in relict areas of Eurasia, as well as North America, provide critical evidence for appraising the origin of the sclerophyllous mediterranean-type vegetation. The Canary Island laurel forest, clearly of tropical derivation (see below), includes numerous shrubs that contribute to the bordering matorral. Most of them inhabited the mainland into the late Pliocene, associated with numerous taxa (*Quercus*, *Punica*, *Arbutus* and *Olea*) that are now confined to mediterranean lands (Depape, 1922, 1928).

There are outposts of mediterranean-type sclerophyllous vegetation in the lower montane belt of the northwest Himalayas in India (Meusel & Schubert, 1971; Mani, 1974; Kitamura, 1964), and also in the north-trending ranges of west Pakistan (Meher-Homji, 1973). In the Pir-Panjal range (alt. 4,500 m), centered about 70 miles east of Rawalpindi in India, the lower southwest-facing flank of the range is covered with thorn scrub composed of *Acacia*, *Carissa*, *Zizyphus*, and their usual associates (Meusel & Schubert, 1971). At slightly higher levels is the evergreen vegetation with species of *Cercis*, *Cotinus*, *Dodonaea*, *Olea*, *Paliurus*, *Pistacia*, *Nerium*, *Quercus*, *Rhus*, *Rhamnus* and others, some of which are deciduous. This community inhabits drier sites, chiefly the deep rainshadow-valleys as near Bhadawar (alt. 1,690 m) and Hardwara (alt. 1,700 m) where there is a reduced rain (Bhadawar) or a long dry summer (Hardwara) because the mountain ridges intercept much of the monsoonal rain. However, Meher-Homji (1973) has noted that in some areas there is (up to 50%) summer rain, notably to the west. The evergreens are replaced above by a *Pinus roxburghii* forest, a pine very closely related to *P. canariensis*. It lies above the laurel forest dominated by evergreens, many of which also contribute to the flora in the Mediterranean region. The *P. roxburghii* forest gives way at higher levels to a mixed conifer forest of *Abies*, *Cedrus* and *Picea*, associated with several oaks, *Aesculus*, *Acer*, *Fraxinus*, *Juglans*, *Populus* and other temperate taxa. This closely parallels the general composition and mode of occurrence of forests in the Mediterranean where the conifers and dicots are represented by very similar species. As noted by Meusel (1971: 70), in the western Himalayas some 40% of the semiarid taxa show relationship to species in the Mediterranean region, though some (*Cercis*, *Cotinus*, *Punica*, *Pistacia*, *Myrsine* and *Zizyphus*) range into subhumid southwestern China and are not restricted Mediterranean taxa.

Nearly a century ago, Hooker (in Hooker & Ball, 1878) suggested that the different races or subspecies of *Cedrus* in the Atlas, Taurus and Himalayan ranges resulted from isolation and extinction of transitional forms in intermediate areas of what may once have been a continuous forest. It is now clear that isolation of *Cotoneaster*, *Olea*, *Punica*, *Quercus* and others along the alpine axis as orogeny and aridity spread during the later Cenozoic has broken up formerly more continuous populations and has resulted in the emergence of closely related taxa (Axelrod & Raven, 1972: 227). In this regard, Meusel (1971) illustrates the

TABLE 3. Some Madrean-Tethyan links, past (*) and present.

Taxa	California	SW US or Mexico	E US	Mediterranean
Arbutus	*menziesii*	*xalapensis*	—	*andrachne*
Buxus	—	*lancifolia*; *mexicana*	—	*sempervirens*
Cercis	*occidentalis*	*occidentalis*	—	*siliquastrum*
Clethra	*(*petiolaris*)	*lanata*	—	*arborea*
Cupressus	*forbesii*	*arizonica*	—	*sempervirens*
Helianthemum	species	—	species	species
Ilex	*(*sonomensis*)	*brandegeei*; *rubra*	—	*balaerica*; *canariensis*; *platyphylla*
Juniperus	*californica*	*deppeana*; *monosperma*; species	*virginiana*	*phoenica*; species
Laurocerasus	*lyonii*	—	*caroliniana*	*lusitanica*
Myrica	*californica*	*mexicana*	*caroliniana*	*faya* (Canarian & Portugal?)
Ocotea	*(Miocene)	*ovoidea*	(*nectandra*; Florida)	*foetans* (Canarian)
Persea	*(Miocene & Pliocene)	*hartwegii*; *podadenia*	*borbonia*	*indica*
Pinus "closed-cone pines" (see text)	*muricata*; *radiata*; *remorata*	*oocarpa*; *pringlei*	*pungens*	*halepensis*; *brutia*
Pistacia	*(Miocene)	*mexicana*	—	*atlantica*; *lentiscus*; *terebinthus*
Platanus	*racemosa*	*racemosa*; *wrightii*	—	*orientalis*
Populus	*fremontii*	*arizonica*; *fremontii*	*sargentii*	*nigra*
Quercus "sect. Ilex" (see text)	*chrysolepis*	*chrysolepis*; *fusiformis*; *virginiana*	*virginiana*	*ilex*
Rhamnus	*californica*; species	species	species	species
Sageretia	*(Miocene)	*wrightii*	*minutiflora* (very rare)	*spinosa*
Sapindus	*(Pliocene)	*drummondii*	*drummondii* (to Arkansas & Louisiana)	*(Pliocene & Miocene)
Styrax	*californica* *officinalis* var.	*jaliscanus*	*americana*	*officinalis*
Zizyphus	*(Miocene)	*obtusifolia*	—	*lotus*

distribution of a number of these across subhumid Eurasia, some of which reach eastward into the drier parts of southwestern China (Table 3). Apart from the sclerophylls, Chatterjee (1947) has also noted that there is a strong influence of east Mediterranean plants in northwest India, where much of the flora from

the Middle East is concentrated, especially members of the Cruciferae and Caryophyllaceae.

The time of appearance of taxa of mediterranean affinities (Table 3) in this region poses a problem because none of the taxa are now known as fossils in the area east of the Caspian. They may have entered northwest India-West Pakistan during the late Miocene or Pliocene. Prior to this, the region evidently was too humid for sclerophyllous plants because the area was then dominated by heavy monsoonal rains. This is indicated by the rich flora in the Karewa Formation at Liddarmarg (alt. 10,500 ft, ~ 3,100 m) on the drier, colder northeast (lee) slope of the Pir Panjal range which rises to 15,000 ft (~ 4,500 m). The flora inhabited the upper Kashmir valley during the late Pliocene (Gansser, 1964: 45–53)—in pre-glacial time—when the valley was bounded on the northeast by the main Himalayan range, while a low ridge—now represented by the lofty Pir Panjal—was on the south (see Puri, 1960: vol. 2: 510). As demonstrated by Puri (1960: vol. 1: 75–80), the flora represents a moist warm temperate to subtropical forest like that now in the outer Himalayas near Murree, on the Simla Hills, and at Mussorrie, which receive heavy monsoonal rain. From paleobotanical evidence, Puri (1946) estimated minimum uplift at Liddarmarg was at least 6,000 ft (~ 1,800 m), though he cited structural evidence (faulting, with displaced Karewa beds now at 13,000 ft) that indicates uplift may have been 8,000–10,000 ft (~ 2,400–3,000 m) since the flora lived.

The outer flanks of the northwestern Himalaya as well as West Pakistan were too moist in the Miocene for mediterranean-type sclerophyllous taxa, as judged from the record now known. As noted elsewhere (Lakhanpal, 1970; Prakash, 1972; Axelrod, 1974), the trend to aridity accounts for major modifications in the distribution of Indian plants since the Miocene. Forests withdrew to the east from the west which is now desert to semidesert, and also from the middle monsoonal area to regions farther east that are ever-wet. As aridity increased, savannas spread at the expense of rain forest, and thorn scrub displaced areas of savanna. India probably was invaded during the late Miocene and Pliocene by taxa of drier requirements from the region farther west, where aridity had appeared earlier. This agrees with evidence noted by Lakhanpal (1970) that the floras from the lower and upper Siwalik beds show a change to a drier climate, as judged from the shift to a flora with much smaller leaves. Pollen evidence (Banarjee, 1968; Lukose, 1969) from the lower and middle Siwalik rocks in Bihar and Punjab shows increasing grains of gymnosperms, notably those of *Pinus* (up to 25%), indicating that during middle Siwalik deposition the Himalayan range had sufficient altitude to support conifer forests. That longitudinal valleys with drier lee slopes were present at this time is consistent with the structural evidence. Thus, sclerophyllous taxa may have been present by the Pliocene, and shifted to the outer northeast-trending valleys as the inner, main Himalayan range was elevated to higher, colder levels in the Quaternary.

The record in southern Eurasia, which is much more complete than that in North America at low–middle latitudes, gives us a reasonably accurate picture of the early history of the sclerophyllous vegetation. As noted by Krystofovich (1954) and Takhtajan (1969), forerunners of sclerophyllous taxa appeared at

low–middle latitudes in the late Cretaceous, when they lived under warm temperate to subtropical climate. Sclerophyllous trees and shrubs had originated there by the early Paleogene, by the close of the Oligocene many species resemble modern ones, and by the middle Miocene most species can scarcely be separated from those now living. This analysis agrees fully with the sequence of events inferred for the history of similar vegetation in western North America (Axelrod, 1958), a region where the record is not so complete.

In summary, the relations suggest that in the Tethyan and Madrean regions semihumid sclerophyllous vegetation (1) has formed an ecotone between tropical and temperate forests throughout its history, (2) that it derived taxa from both sources, though chiefly the former, (3) that it had a wider distribution in the past, covering areas presently too dry for it, and (4) that the present restricted distributions reflect selection and segregation in response to the development of new dry climates during the Quaternary.

EVOLUTION OF ADAPTATIONS

Structure.—Sclerophyllous woody taxa in regions of mediterranean climate have small, thick, sclerophyllous evergreen leaves, often with a villous covering, and frequently with a thick cuticle and sunken stomata, all of which enable them to conserve moisture during the long period of drought. In addition, they have hard wood ("hard chaparral" of Jepson, 1925: 6), and deep root systems that provide a means to tap water at deep levels during the period of drought. Furthermore, many of the shrubs and small trees regularly sprout following fire, so that the slopes are quickly covered again with a dense cover.

These structural adaptations are not unique to plants of mediterranean-type climates. Many of the same species range into regions with summer rainfall (Table 1), a condition like that under which they lived in Neogene time. The origin of these structural adaptations becomes apparent when we realize that taxa with xeromorphic structures now occupy diverse environments. These include ever-wet tropical rainforests, montane rainforest, and evergreen microphyllous scrub at timberline. They also inhabit subhumid to semiarid landscapes where they contribute to sclerophyllous woodland and scrub (chaparral, macchia, fynbos) that grade into more mesic laurophyllous forests in which sclerophyllous taxa are also common. Such diverse occurrences by taxa that belong to numerous wholly unrelated families implies that the sclerophyllous habit must be ancient and recurrent. This agrees with the occurrence of many sclerophyllous taxa in diverse environments of Cretaceous and Tertiary times. Some of the oldest fossil leaves that have been attributed to angiosperms are sclerophyllous nanophylls from the Shasta series (Hauterivian-Barremian transition: ~ 127–128 m.y.) of northern California. Since the basic adaptive structural features—sclerophylly, deep root systems, stump sprouting, thick epidermis—occur repeatedly in diverse taxa in numerous dissimilar environments, of which Mediterranean-type habitats are only one, broadleaved evergreen xeromorphic plants can scarcely be considered "specialists." Contrary to most ecologists, I believe they may best be regarded as "generalists."

The structural features of evergreenness, sclerophylly, deep root system, etc.

appear to have originated under relatively warm, moderately mesic conditions at least, and appear to have preadapted taxa to climates of lower rainfall, a shorter rainfall period, and greater ranges of temperature. Sclerophyllous evergreen leaves are not only ancient, they may well be a primitive feature of angiosperms. The basic modifications in terms of adaptation to different climates have been minor changes in structure, such as reduction in size, formation of deep internal crypts, and thickened cuticle or waxy covering, to reduce water loss in areas of restricted precipitation and high evaporation. Such modifications are ancient, as judged from the presence of essentially modern evergreen chaparral and woodland taxa in Miocene and Oligocene floras which lived under ample summer rain. Clearly, these features are not an evolutionary response to an ancient, persistent mediterranean-type climate, as many have implied.

The outstanding Australian geologist-naturalist, E. C. Andrews (1913, 1914, 1916) was one of the first to perceive the general evolutionary relations of xeromorphic plants. He noted that in Australia xeromorphs are confined to drier areas characterized by coarse, mineral-poor sandstones. These are now known to be the result of sedimentation on stable shelves in which the unstable minerals (with necessary elements for plant growth) are gradually eliminated, leaving rocks like quartz sandstone, quartz-glauconite sandstone, quartz muscovite sandstone, clay shale, and siltstone with quartz. These sites are largely inhabited by the unique Australian taxa, including *Banksia*, *Callistemon*, *Candollea*, *Darwinia*, *Epacris*, *Leptospermum*, *Melaleuca*, *Persoonia* and a host of others. The mineral-deficient areas are surrounded by rich, sheltered, well-watered valleys in which the taxa are not peculiarly Australian, but are wide-spread, such as *Elaeocarpus*, *Eugenia*, *Ficus*, *Livistonia*, *Myrtus* and many others. He inferred adaptive radiation in Australia involved the perfection of structural adaptations of the unique xeromorphic taxa to the sandy, extremely siliceous, mineral-poor ("hungry soils") substrate, and that this adaptation has been proceeding in many groups since the middle Cretaceous at least.

Beadle (1966) presented further evidence that adaptation to low-fertility soils, and particularly those low in phosphate, has resulted in the evolution of new taxa by accentuating xeromorphic characters (*contra* Loveless, 1961, 1962). This may involve reduction of leaf size and structure, or a reduction in aerial parts, or increased proportion of non-living to living tissue, or seasonal growth and dormancy by underground perennating root tubers. He also suggested lineages with lower nutrient requirements probably adapted to areas of lower fertility early in angiosperm history, so that the relationship between taxa in sites of low fertility and those living on more normal substrates is now remote in many cases. The xeromorphs on low-fertility soils are adapted in most cases to a limited phosphate supply, which also determines levels of soil nitrogen. Thus, the low fertility of Andrews's "hungry soils" excludes plants with higher nutrition requirements, and enables the xeromorphs to exploit them. This exclusion principle applies also to other substrates, notably limestone, serpentine, and other rock types.

The habit of stump-sprouting has been assumed to be of pyrogenic origin (Jepson, 1925: 6; Hanes, 1971; Sampson, 1944). Actually, many of the woody plants in laurophyllous forests that survive under moist, warm temperate climate,

have this character as do species in these forests that have related taxa in chaparral-macchia. Crown sprouting probably is an ancient trait among angiosperms to judge from the fact that most woody plants do stump-sprout, and the habit is found in all climatic areas that support woody taxa of diverse origins. From an evolutionary standpoint, Wells (1969) has shown that over 75% of the species of *Arctostaphylos* (59 of 75 species) and *Ceanothus* (46 of 58 species) in California have lost the habit of stump sprouting. He suggests the change in mode of reproduction to one by seeds has resulted in a greater frequency and intensity of selection, and has quickened the tempo of evolution in major sections of these genera. The increased diversity of non-sprouting species, most of which are narrow endemics and separated by only minor characters, probably commenced late in the Tertiary as judged from topographic-climatic relations.

The evolution of plant form that allows a relatively large proportion of the limited rainfall to reach the soil surface in the form of stem flow (reviewed in Mooney & Dunn, 1970), also appears to be an ancient character. Plants with stiff, upright branches and smooth bark obviously have greatest stem flow, which yields a slow and steady supply of moisture at the base of the shrubs. This character could not have originated under mediterranean climate inasmuch as many of the taxa are known from the Miocene. The adaptation may have originated in response to monsoonal climate in the understory of laurophyllous forests—where the same adaptations occur today. To judge from the fossil record, the adaptive shift in terms of evolution of structural characters had already taken place in many alliances by the middle Eocene. This presumably occurred in local, exposed sites in a terrain of more mesic aspect (Stebbins, 1952; Axelrod, 1967*c*), as well as in dry edaphic sites wherever these were present (Axelrod, 1972).

The origin of taxa of lower stature (small tree to shrub) and with smaller leaves (microphyll-nanophyll-leptophyll-aphyllous) from those in mesic evergreen forest and woodland scarcely poses an evolutionary problem. Adaptations of this nature are well established by sequences that can be observed today. In taxa that have a wide range, size decreases from small trees in moist equable areas, to shrubs in the drier interior or in more exposed and rocky situations, as shown by *Garrya ovata*, *Cercocarpus mojadensis* and *Mahonia fremontii* in Nuevo Leon; by *Rhus ovata*, *Cercocarpus montanus*, and *Quercus turbinella* in central Arizona; or by *Heteromeles arbutifolia*, *Prunus ilicifolia* and *Quercus dumosa* in coastal California.

Not only is there a decrease in stature, adaptation to drier areas has involved other structural features, notably a trend to smaller leaves, more sunken stomata, thicker cuticle, denser villous covering, etc. Such modifications occur today in taxa that range from mesic coastal or insular sites to drier, more extreme interior regions. They are well illustrated by geologically new phylads, as exemplified by species of *Ceanothus* (Nobs, 1963) in the north Coast Ranges of California that have originated since the late Pliocene (3.5 m.y.); by species and varieties of *Cercocarpus* in California (Mortenson, 1973); by species of *Quercus* that are typical trees of woodland and savanna (*Quercus agrifolia*, *wislizenii*) or woodland (*chrysolepis*) vegetation, but occur as shrub varieties in chaparral. These scrub oaks are found chiefly on edaphically drier sites with poor thin soil, or on notably

rocky sites, but occasionally on markedly different substrate, as in *Q. durata* on serpentine.

Current studies of California chaparral in terms of morphological changes within the vegetation type provide information in terms of adaptive responses (Mooney & Dunn, 1970; Mooney & Harrison, 1972; Mooney *et al.*, 1974). In the Sierra San Pedro Martir, northern Baja California, morphological features vary systematically with increasing moisture and decreasing temperature as altitude increases. Evergreen species become more important with increased altitude, leaf size increases, vertically-oriented leaves become more frequent, and leaves become more sclerophytic. Sclerophylls also increase as water stress decreases with altitude since photosynthesis can occur all year and it is "advantageous" not to replace the entire leaf crop each year. The leaves become larger and more sclerous at higher altitudes because water availability and lower temperatures reduce the likelihood of leaf overtemperature. At lower altitudes where there is less moisture and where leaf temperature may exceed that of the air, leaves are typically smaller, species of drought deciduous coastal sage increase, and so do succulents. These features closely parallel a gradient from the Canarian laurel forest down to the drier and hotter desert which also has numerous sage species, as well as succulents.

Function.—Functionally, adaptation to mediterranean climate represents a fine attunement with respect to the ability to reproduce (flower, set seed, germinate, establish) within a relatively brief period of moist climate during the cooler part of the year. In this regard, it is recalled that the coincidence of cool wet winters and hot dry summers is the distinguishing feature of mediterranean climate. Winter is not the chief period of rest, nor is summer the principal time of activity for vegetation as in areas farther north (Oregon, central Europe). Drought in summer is the main limiting factor to plant activity, not winter cold. As emphasized recently by Bailey (1972), frost and snow are rare to absent in areas with mediterranean climate, and winter rain is adequate for sclerophyllous vegetation. Thus, flowering and growth occur chiefly in winter and spring, and only a few species and rare individuals of typical mediterranean vegetation flower and grow in summer. This occurs notably in the milder coastal strips—often fog-bound—where the stress of high evaporation is reduced.

A clue to the evolution of functional relations of chaparral taxa is provided by the occurrence of the same species in areas of summer rain (eastern Mexico), or summer and winter rain (Arizona to New Mexico), as well as in a region of prolonged summer drought (California). As listed in Table 1, numerous species (and varieties) are common to the chaparral of southern California and central Arizona, and some of them (*Arctostaphylos pungens*, *Ceanothus greggii*, *Mahonia fremontii* and *Rhus trilobata*) range to Nuevo León in eastern Mexico where rainfall is in summer, not winter. Climate in areas with summer rain parallels that indicated for the Miocene and Pliocene of California where summer drought now prevails, though temperature was not so extreme in the Neogene in California. Ample summer precipitation in the Miocene of southern California is indicated by the occurrence there of *Bursera*, *Clethra*, *Persea*, *Pithecolobium*, *Quercus* (some spp.), *Robinia*, *Sabal* and others that live today only in areas with warm-season

precipitation. They disappeared as summer rainfall decreased during the Pliocene and early Pleistocene as the ocean chilled, and as the thermal contrasts between land and sea increased.

A similar pattern occurs in the Mediterranean region. Numerous sclerophyllous species of the macchia and woodland extend from Spain to northern Turkey where there is summer rain, and some (or their varieties) range discontinuously farther east into the Himalayan region where rainfall is chiefly in summer (Meusel & Schubert, 1971; Meusel, 1971; see below). Apart from Spain-northwest Africa-southern Turkey-Israel, the period of summer drought in the Mediterranean area is not so prolonged as that in California. As noted earlier, relatively heavy rain continues into June and commences abruptly again in October, whereas in California precipitation gradually tapers off to the long dry season and then increases gradually in autumn.

The present distribution of sclerophyllous taxa that range from areas of summer rain into those with summer drought provides a basis for understanding functional responses in the latter area. Obviously, the taxa that occur in both regions have adapted to summer-dry climate more recently. This could be accomplished by shifting the time of seedling germination and establishment from late spring–early summer to the late winter–early spring, coupled with appropriate physiologic adjustments for the times required for growth, flowering and seed maturation. It is known (Hanes, 1965; Mooney & Parsons, 1973) that as moisture supply becomes restricted and limited in early summer (June), chaparral taxa become dormant or nearly so, and by August–September plants are operating at only 4–5% of their wet season maxima. At the same time in Arizona, 12 of the *same species* that also make up the chaparral there must be operating at peak efficiency under high rainfall and temperature, much as they are presumed to have done during the Neogene in California.

In this regard, Walter (1973: 121) points out that the significance of sclerophylly is that the taxa can conduct gaseous exchange in the presence of adequate water supply, but can also cut it down radically by closing the stomates when water is scarce; measurements of transpiration show that water losses in summer are 3 to 6 times greater in wet than in dry habitats. This control enables sclerophylls to survive periods of drought with neither alteration of plasma hydrature, nor reduction of leaf area, so that when rains recommence in autumn, the plants resume production immediately. Hence, they compete successfully in winter-rain regions with non-sclerophyllous evergreen species that are sensitive to drought, as well as with deciduous trees. This implies again that a dormant summer period due to drought was not a feature of the ancestral taxa, a view consistent with the paleoclimatic record. Thus, it seems that sclerophylly (or near-sclerophylly) is a fundamental adaptation of great antiquity, and that it can (and has) developed various functional means for coping with limited moisture as well as with other environmental needs. The same sclerophyllous species that live under summer drought (California) as well as winter drought (Nuevo León), clearly indicate the potential for functional adaptation. This suggests again that broadleaved sclerophyllous taxa are "generalists", having basic structures that have been functionally adaptable to diverse environments.

In the Madrean-Tethyan region, the shift in functional adaptation may have been originating in the Pliocene as summer rains commenced to decrease, or it may have developed gradually and intermittently during the warm-dry phases of the interglacial ages, or it could be younger, with the taxa representing very new ecotypes that originated in response to the recent extreme drought. Comparative physiologic studies of the responses of different populations of taxa that occur in California-Arizona, or Spain-northern Turkey, may provide insight into the functional differences between the living populations, and hence an understanding of their origin.

In this regard, comparison of the mediterranean-type climates of California, Spain and Chile with those in Australia and South Africa reveals significant differences (Emberger, 1930, 1933; Walter, 1968; Aschmann, 1973*a*; Raven, 1973). In Australia, seasonal flowering in the sclerophyll vegetation is chiefly in spring, but vegetative growth of shrubs continues through the drought period, whereas it is largely confined to spring in California, Chile and the western Mediterranean (Specht, 1969; Mooney & Dunn, 1970). However, in South Africa rainfall is distributed more evenly through the years, there is at least 0.7 inches rain in each summer month, there is no severe summer drought, and flowering in the fynbos is rather continuous through the year in this highly equable climate. This finds a parallel in the mildest parts of the coastal strip of California (Inverness at Tomales Bay) or Turkey (Inebolu to Sansum) where flowering of evergreen sclerophyllous shrubs continues sporadically through summer and into autumn. There is an implied gradient in these areas of mediterranean-type climate, from a transitional condition with no significant drought (South Africa; N. Turkey) to one in which it is moderate (Australia), to one that is severe (Spain, California). In terms of functional responses, these are precisely the stages through which taxa that make up sclerophyllous vegetation passed during the late Pliocene and Quaternary, as the mediterranean condition gradually developed.

A current article by Seddon (1974) presents a valuable review of the problems raised by terminology of sclerophyllous taxa and vegetation, and the role of soil nutrients and other factors controlling the distribution of sclerophyllous forest and rainforest in Australia. The review mentions additional data consistent with the thesis that sclerophylly is an ancient character, and not one that is attributable to evolution under mediterranean climate. Thus, Specht & Rayson (1957) note that in South Australia and West Australia many taxa have a growth phase out of rhythm with the present mediterranean-type climate, making their major growth during the driest summer months. Further, Burbidge (1960) has suggested that these growth rhythms appear to belong to climates of earlier (*i.e.*, Tertiary), more humid times, and similar observations have been made with respect to the sclerophyllous Cape flora of South Africa, elements of which also extend into summer rain regions (Levyns, 1964). Further, in a current manscript Johnson & Briggs (1975) also emphasize that sclerophyllous vegetation is not restricted to areas of mediterranean climate in Australia or South Africa, but may range into summer rainfall regions as well. Their review of the available evidence leads them to speak of the "mediterranean myth" so far as the restriction of sclerophyllous taxa to mediterranean climate is concerned, a view that most ecologists

have held since the days of Schimper. These data further support the notion that sclerophylly is one of several linked characters (deep roots, crown sprouting, etc.) common to many angiosperm families, and probably of ancient (Cretaceous) age, that tend to endow an alliance with the characteristics of "generalist"—enabling it to adapt readily to diverse environmental conditions, of which the mediterranean-type climate is evidently the most recent.

In summary, the adaptations of diverse taxa of sclerophyllous evergreen shrubland (chaparral, macchia, matorral, fynbos) represent ancient structural features inherited from ancestors in laurophyllous forests. The functional adaptations in response to mediterranean climate have evolved more recently. Some taxa have ecotypes that live in both summer-wet and summer-dry areas, but the endemics now in mediterranean-climate areas may easily have adapted to this condition by shifting the period of flowering and growth into the early part of the year.

RISE OF CHAPARRAL-MACCHIA

The remains of many sclerophyllous shrubs that characterize chaparral vegetation in California (*i.e.*, *Arctostaphylos*, *Ceanothus*, *Cercocarpus*, *Garrya*, *Quercus*, *Rhamnus* and *Rhus*) and the similar macchia of the Mediterranean region (*Arbutus*, *Ilex*, *Myrtus*, *Phillyrea*, *Pistacia*, *Quercus* and *Rhus*) are now known from the fossil record. According to accepted principles of paleoecology (Clements, 1916, 1936; Chaney, 1938; Cain, 1944: Chaps. 5,6), which are based on the adage "The present is the key to the past," the occurrence of several sclerophyllous shrubs in a fossil flora implies chaparral (or macchia) probably was a well-developed climax on nearby slopes. Although this principle forms the basis for the opinion that chaparral formed climax vegetation during much of Tertiary time (*i.e.*, Clements, 1936; Dorf, 1930; Axelrod, 1937, 1958, 1973; Becker, 1961; MacGinitie, 1953), several lines of evidence now cast doubt on its validity. In the first place, the fossil floras that are presumed to have had prominent chaparral come from areas where topographic diversity was insufficient to support it as well as thorn scrub, oak savanna-woodland, and bigcone forests (*i.e.*, Mount Eden flora, Axelrod, 1937), or thorn forest, oak woodland, mixed conifer forest and subalpine forest (*i.e.*, Ruby flora, Becker, 1961; Florissant flora, McGinitie, 1953), or laurel forest, sclerophyll woodland, and mixed deciduous forest (Theziers flora, Boulay, 1890), and still enable plants from all these vegetation-climatic belts to contribute importantly to the record. Secondly, sclerophyllous shrubs that make up chaparral (and macchia) regularly form the understory of adjacent oak, or oak-pine-laurel woodland with which it typically alternates on adjacent slopes. Clearly, if a fossil flora has numerous sclerophyllous shrubs, as well as oaks, pines, madrones, and laurels that obviously formed a sclerophyllous woodland, the shrubs may only have formed a rich understory in it, rather than contributing chiefly to chaparral. And thirdly, examination of sclerophyllous vegetation in the subhumid parts of the United States, Mexico, and the extended Mediterranean (Tethyan) region shows that in every area there are numerous transitions from sclerophyll woodland with a rich understory of shrubs and small trees, through scattered woodland trees in sclerophyllous shrublands, to essentially pure chaparral- or macchia-covered slopes.

Since all these stages commonly occur in proximity and are regularly gradational, it is apparent that sclerophyllous shrublands are basically successional, whether in regions of severe summer drought (California, Spain), or ample summer rain (Arizona, Nuevo León, N. Turkey). The data suggest chaparral and macchia formed only local brushlands that were basically seral to woodland during the Tertiary, although local edaphic sites were temporarily favorable for shrubs. The initial spread of extensive brushlands most probably coincided with rapid uplift of mountains with steep slopes during the late Pliocene and Quaternary (Axelrod, 1958: 498).

Tectonism.—Commencing in the later Pliocene, intense orogeny affected the regions where chaparral and macchia are prominently developed today. This not only includes California (with uplift of the Sierra Nevada, Coast Ranges, Transverse and Peninsula ranges), but central Arizona-New Mexico (uplift of Mogollon Plateau), and eastern Mexico (uplift of Sierra Madre Oriental). Furthermore, the extended mountainous alpine systems reaching from the Mediterranean eastward through Turkey and Iran to the Himalayas, was also uplifted late in the Cenozoic.

The rapid appearance of steep mountain slopes in areas of subhumid climate favored the spread there of shrubs over trees. Owing to natural updrafts, fires resulting from lightning or volcanism would now be more effective than in the earlier terrains of gentle relief. However, most slopes would soon revert chiefly to woodland with a rich sclerophyllous understory of small trees and shrubs, as can be seen today in numerous relict areas (see lists above). In some unique edaphic situations [*i.e.*, marble outcrops in a granitic terrain; serpentine; metamorphosed Archean basement intruded by younger plutonics; acidic volcanic rocks (*i.e.*, rhyolite) overlying carbonates], shrubs no doubt were favored, as they are today. Although such areas of chaparral and macchia may have formed local "edaphic climaxes," they were relatively subordinate and probably transient with respect to woodland—even on outcrops of ultrabasics, as may be seen today in many areas in California.

Climate.—The spread of local patches of chaparral at the expense of woodland was increasingly favored by the drier climates of the later Quaternary interglacial ages. Since summer rainfall characterized regions of present mediterranean climate into the early Pleistocene, the adaptive advantage of a shrub- over a tree-habit has appeared only recently. In areas of present mediterranean climate the lowlands were under pluvial conditions during the ice ages. At these times, chaparral and macchia were restricted to the advantage of forest and woodland. This is shown by the early Pleistocene record in southern California where forest descended fully 3,000 ft to the floors of the interior valleys that are now surrounded by chaparral-covered mountain slopes (Axelrod, 1966). In Tunis-Algeria oak woodland and macchia shrubs descended into regions presently desert (Arambourg *et al.*, 1953). Clearly, areas of chaparral and macchia in the present regions of mediterranean climate were not so large in the ice ages, or the Neogene, as today.

Progressively drier climates developed during the successive interglacial ages

because mountains were being elevated creating rainshadows, and stronger temperature contrasts were developing as the oceans became colder. As a result, the high-velocity, hot and dry winds (santa anas; siroccos) that descend from the continental interior into areas of mediterranean climate during the late summer and autumn were progressively strengthened during the later interglacials. At such times humidity is very low, there is little moisture in the soil, and these times of drought and potentially high fire hazard favor sclerophyllous shrubs, especially on drier slopes. The most favorable time for *natural* chaparral expansion probably was during the Xerothermic (Hypsithermal) period (8,000–4,000 BP) when climate was drier and warmer than at present. In California, numerous xerophyllous taxa spread from the interior to the coastal strip, and some still survive there on warm, exposed slopes (Axelrod, 1966: 42–55). We may infer that "santa ana weather" was more pronounced during the Xerothermic period than at present, and that natural fires fanned by high winds in terrains of steep slopes would have favored the temporary spread of brush over woodland. As climate moderated in more recent times, woodland trees reestablished in areas formerly brushland.

Fire.—Chaparral is maintained by fire today, its frequency determining if oak woodland or chaparral or grassland dominates, especially on the drier south-facing slopes. Total incineration of trees and shrubs by raging fires on steep slopes greatly accelerates erosion during heavy rains in the following wet seasons. This makes conditions unfavorable for trees by removing soil and litter, and creating dry barren to semibarren outcrops wholly stripped of soil. The spread of chaparral is especially favored by the great fire storms that rage late in the year when humidity is very low, when soil moisture is low, and when brisk to stiff (20–30 mi/hr) winds (santa anas, siroccos) are prevalent and continue for several days. These conflagrations that leave slopes totally devoid of plants create temporarily more arid conditions by the burning of litter, the reduction of mineral matter, and the removal of soil following heavy rain. Clearly, shrubs are favored over trees, though some (oak, pine, etc.) may persist in protected canyons or on favorable (north) slopes, as may be seen today in numerous areas (see lists above).

Following fire, shrubs often sprout prior to the first rain, and may cover the slopes rather quickly. However, it is doubted that this adaptation originated in response to fire (*cf.* Jepson, 1925: 7). As discussed earlier, the sprouting habit is frequent in many woody plants in mesic sclerophyllous forests where fire is not frequent, forests which (ancestrally) produced the taxa that contribute to sclerophyllous oak woodland and chaparral today. Although fire became more frequent as steep slopes arose in the Quaternary, and especially during the drier parts of the interglacial ages, the conditions that perpetuate chaparral today are largely the result of man's diverse activities, of which fire is only one.

Man.—Study of the rich herbaceous vegetation that "suddenly" appears after fire has swept areas of chaparral in the Coast Ranges of California shows that the seedlings largely are from viable seed present in the soil *before* fire, and not from dispersal from adjacent open areas (Sweeney, 1956). Of the 217 annuals identified in chaparral burns, Sweeney (1956: 193–205) reports 196 are common in adjacent open sites where they contribute to grassland or to oak-savanna vegetation. This

implies chaparral has invaded areas that formerly were open, which is consistent with evidence in other areas that shrubs spread into grassland following overgrazing—which is prevalent in the Coast Ranges. Isolated patches of grassland and oak savanna that regularly alternate with chaparral in the Coast Ranges and Sierra Nevada foothill belt lend further support to this interpretation. Furthermore, a good herbaceous cover appears after fire in the more extensive brushlands of southern California (Horton & Kraebel, 1955: 258). In addition, relict patches of oak-grassland (or oak-walnut grassland) are in the chaparral zone. They are in the Piru Mountains near Oak Flat Guard Station; near Whiteacre Peak to the west; on Hwy. Interstate 5 at the head of Weldon Canyon 2.5 mi south of Newhall; in the Santa Monica Mountains, in shale-valleys and on cooler canyon slopes; in the San Gabriel Mountains near the mouth of Dalton Canyon; south of Palomar Mountain to Roderick Mountain; and also rather widely in San Diego County. In this regard, Dodge's (1975) study of vegetation associated with fire history in San Diego County shows that the region was largely open in the early days. As judged from reliable historical records, the spread of chaparral corresponds to the introduction of heavy grazing by cattle and sheep on the coastal slope in the late 1700's, and in the back country after the 1850's. At that time, patches of chaparral were confined chiefly to local rocky sites and to those of shallow soil, as is inferred here for the Neogene and earlier times as well.

Additional evidence that sclerophyllous shrublands (chaparral, macchia, matorral) as well as sage and semidesert scrub have largely spread under man's aegis, has been discussed by Aschmann (1973*b*) for Latin America, by Darby for Europe (1956), and also by Naveh & Dan (1973) for Israel. In this regard, it is significant that in the Izmir region (Menemen to Kusadasi) where rainfall is only 25–28 inches (640–710 mm), reforestation of the semibarren landscape covered with a degraded macchia is progressing readily. The native *Pinus brutia* is planted in the fall just as the rains commence. The trees grow rapidly and readily in what obviously was once their native landscape (as judged from relict stands) prior to clearing for lumber and agriculture, and subsequent degradation by grazing (goats, sheep) and resultant erosion.

My brief observations across the subhumid parts of much of the Madrean-Tethyan region indicate sclerophyllous shrublands are largely man-made, and are not a climatic climax, either in areas with summer drought or summer rain. This agrees with the view expressed by Turrill (1929) that extensive brushlands (of the Balkan peninsula) are "rarely if ever natural climatic climaxes. They either represent the undergrowth of forests from which the high trees have been removed by lumbering or other modes of destruction, or they are stages of subseres (p. 144). . . . (Macchie) is often historically the undergrowth of destroyed forests, frequently of *Pinus halepensis* (or *brutia*) (p. 144). . . . The macchie are very frequently themselves a stage in a subsere started by the biotic factor of human activity. It is certain that for extensive stretches of lowland and hill zone in the Mediterranean domain the natural climax formation is *Pinus halepensis* high-forest with macchia undergrowth. All stages between this and treeless macchie may be studied in Greece and other parts of the Mediterranean domain (p. 146). . . ." A similar view is expressed by Hooker (in Hooker & Ball, 1878: 20).

"The scarcity of trees in this country (Morocco) is mainly due to the mischievous interference of man. The same ignorant greed of the herdsman, who to procure a little meagre herbage for goats sets fire to wide tracts of brushwood, that has reduced whole provinces of Spain to a desert condition, has been equally busy and equally effectual in Morocco." The recent study of Crete by Zohary & Orshan (1965: 13) reaches a similar conclusion. "The present vegetal landscape of Crete is largely the outcome of man's intereference during millenia. As at present, . . . forests are unable to regain their area. . . . Nowadays the evergreen xerophyllous . . . maquis and garigue dominate. They suggest that the tremendous change of vegetation both in distribution and composition that took place . . . is due to man's destructive activity." Similar conditions also are well documented for Greece in recent works by Harris & Vita-Finzi (1968) and by Higgs & Vita-Finzi (1966). As the latter have pointed out (Higgs & Vita-Finzi, 1966: 29): ". . . the erosion of the soils from the hills, which . . . had begun at least as early as Middle Palaeolithic times, had probably by Neolithic times already decreased the pasturage potential. . . . That such a change had taken place was noted by Plato (who wrote) 'During these 9,000 years many severe storms have occurred and the soil swilled away from the higher regions . . . leaving only the skeleton of the land. . . .'" A very similar story can be pieced together across the southwestern United States and adjacent Mexico, whether in the summer-dry western, or in the summer-wet eastern part of the region.

BIOGEOGRAPHY

Broadleaved sclerophyllous vegetation appears to have had a similar history in North America and Eurasia. Its taxa, which originated from ancestors in mesic evergreen forests, adapted to expanding dry climate across low–middle latitudes. By the later Paleogene, sclerophyllous vegetation formed a broad, nearly continuous belt across each continent. It was then restricted by spreading drier and colder climates to relict areas of subhumid, mild-winter climate. Decreasing summer rain in the west eliminated taxa from the emerging mediterranean-climate areas, confining them to the eastern, summer-wet regions. This history of the broadleaved sclerophyllous belt bears directly on three problems that are now considered. The first pertains to an explanation of the floristic links between sclerophyllous vegetation zones in North America and Eurasia (Axelrod, 1972, 1973); the second concerns the relation of the spreading sclerophyllous zone to the problem of the disjunct "Appalachian" deciduous hardwoods in the Mexican cloud forests; and the third raises the problem of the relation between the sclerophyllous zone and source of the Canary Island laurel forest.

MADREAN-TETHYAN LINKS

As noted earlier, taxa now common to the sclerophyllous floras of California and the Mediterranean region include species of *Arbutus*, *Cercis*, *Cupressus*, *Juniperus*, *Helianthemum*, *Myrica*, *Pinus*, *Platanus*, *Prunus* (*Laurocerasus*), *Quercus* (evergreen) and *Styrax*. In addition, the summer-wet region of Arizona-New Mexico has species of *Bumelia*, *Cercis*, *Platanus*, *Sageretia* and *Sapindus* that are either represented by related taxa in the Mediterranean region, or occurred

there and in California-Nevada during the Neogene. Furthermore, in the Sierra Madre of Mexico, the latter genera are now associated with *Arbutus*, *Clethra*, *Ilex*, *Myrica*, *Persea*, *Pistacia* and *Sabal* that either occur in the Mediterranean region today, or were there and also in California during the Neogene—and presumably earlier as well.

An example of this relationship is provided by the early Miocene (Burdigalian) flora of Majorca (Arenes & Depape, 1956), dominated by broadleaved sclerophyllous taxa. These include *Phoenix* and *Sabal* among the palms, and evergreen dicots such as *Laurus*, *Myrica*, *Persea*, *Pistacia*, *Quercus*, *Sapindus* and *Zanthoxylum* that are similar to living species and are represented by related (ancestral?) taxa in the Oligocene and Eocene floras of southern Europe (lists in Arenes & Depape, 1956). Most of the fossils are allied to species in the American Miocene and Oligocene. The Majorca flora compares well in general physiognomy with the evergreen oak-laurel-palm woodland of coastal southern to central California, as represented by the Carmel, Puente and Modelo floras. The following genera in the Miocene of southern California have rather similar species in the Majorca flora—*Sabal*, *Myrica*, *Persea*, *Pistacia*, *Quercus* and *Zanthoxylum*, and *Sapindus* is represented in the Pliocene there.

Additional links with the Mediterranean region appear to be represented in the American Paleogene floras; few were identified by earlier workers probably because they were not searched for. In this regard, Moore (1973) gives credence to the record of *Phoenix* in the Eocene of Texas (Berry, 1914). *Zanthoxylum* (= *Fagara*) in the late Eocene-Oligocene of the Gulf States (Berry, 1916*b*, 1924) has comparable species in the Miocene-Oligocene of the Mediterranean, and in the Mint Canyon flora of southern California as well. In the drier interior, several species in the Eo-Oligocene Florissant flora (MacGinitie, 1953) of Colorado display relationship with those now only in the Mediterranean region, or in Mexico- the Mediterranean-southwest Asia. Among these, *Quercus orbata* appears similar to the fossil *Q. cruciata* of southern Europe; *Cotinus fraterna* resembles *C. coggygria* of the Mediterranean pine-oak woodland and macchia that ranges east into China; *Rhamnites pseudo-stenophyllus* shows relationship to *Rhamnus* in California (*R. rubra*), eastern Mexico (*R. pinetorum*), and the Mediterranean (*R. oleoides*, *R. lycioides*); and *Daphne septentrionalis* resembles *D. oleoides* of the Mediterranean scrub and *D. giradldi* or *D. tangutica* of western China. The Oligocene *Platanus stenoloba* from Montana (Becker, 1969) shows considerable relationship to *P. orientalis* of the eastern Mediterranean, as well as to its nearest relative, *P. racemosa* of California and Baja California.

In California, the Chalk Bluffs flora of early Eocene age is reported to have *Nerium* (MacGinitie, 1941). The leaf of *Myrtus oregonensis* from the Miocene of central California has been compared with leaves of the living Mediterranean *M. communis* Lesquereux (1883), but the resemblances now appear largely superficial (H. Schorn, oral communication, June, 1974). The widespread *Arbutus idahoensis* in the Miocene of the West shows affinity with *A. canariensis*, though it has shorter petioles. It was a regular member of broadleaved sclerophyll vegetation in the Miocene, and was associated with sclerophyllous trees and evergreen shrubs (*Ceanothus*, *Cercocarpus* and *Heteromeles*) in the Pliocene. In

the Blue Mountains flora it is recorded with *Pinus tiptoniana*, represented by several cone impressions and numerous 2-needled fascicles that closely resemble those of the living *P. halepensis* and *P. brutia* of the Mediterranean sclerophyllous zone (Chaney & Axelrod, 1959). The madrone and pine evidently contributed to a broadleaved sclerophyll vegetation with *Quercus* and *Lithocarpus* on warmer slopes adjacent to a mixed conifer-hardwood forest that inhabited moister, cooler sites in the region.

Apart from these, fossil live oaks in southern Europe are considered by Andreánszky (1962*b*) similar to taxa (sect. Virentes: *cf. Q. virginiana, virens*) now in the coastal Atlantic and Gulf States. In their analysis of the early Miocene (Burdigalian) flora of Majorca, Arenes & Depape (1956) note that *Q. drymeia* resembles some Mexican oaks (*Q. xalapensis, lancifolia, sartorii*), and that *Myrica balearica* shows some relationship to *M. california* and to other species as well. Several authors (*i.e.*, Grangeon, 1958; Arenes & Depape, 1956) have compared *Quercus elaena* with *Q. phellos*. All these specimens should be reexamined so as to verify the suggested relations.

The data suggest that an ancient sclerophyllous flora adapted to subhumid climate inhabited lower–middle latitudes in the Paleogene, stretching along the shores of the Tethyan region and across southern North America (Fig. 1). The links are relicts of effective migration across the middle Atlantic, for it was narrower in the Paleogene (Phillips & Forsyth, 1972; Dietz & Holden, 1970). Dispersal was aided by micro-continents (Azores), and by volcanic islands along the mid-Atlantic Ridge and its flanks that were rafted subsea as the ocean basin widened and deepened. In addition, migration during the Paleogene was favored by the lower latitude of the east coast (Fig. 1), and especially by the ENE orientation of the Appalachian axis, having since been rotated to its NE trend (Phillips & Forsythe, 1972; Walper & Rowett, 1972). This orientation (Fig. 2) produced more numerous warm, dry sites for migration, especially on granite-gneiss domes, "shale barrens," and other suitably hard rocks scattered through the Piedmont.

That land areas at low–middle latitudes had warm, subhumid climate is indicated by latitudinal position marginal to the subtropical high pressure belt, marked now by the Azores High. This belt of dry descending air extended farther west during the Paleogene than at present. North America was low, high cordilleras had not yet been elevated, the Americas were widely separated by ocean, the Tethys was broad, and the global latitudinal thermal gradient was much less than that of today—all implying a broader zonal distribution than now exists. A belt of dry climate is confirmed by the thick evaporite sections in the late Cretaceous and Paleogene of the Gulf States (Green, 1961; Lotze, 1964; Kozary *et al.*, 1968), in northern Mexico (Imlay, 1944), and in the western interior as shown by the Green River Formation (Bradley, 1948, 1964), as well as in the Paleogene from Spain to India and southwest China (Strakhov, 1960; Green, 1961; Lotze, 1964; Kozary *et al.*, 1968). Furthermore, the fossil floras of all these areas have comparatively small- to moderate-sized sclerophyllous leaves (see Berry, 1916*b*, 1924; MacGinitie, 1969; Dilcher, 1973; Andreánszky, 1962*a*, 1962*b*; Arenes & Depape, 1956; Grangeon, 1958; Vasilevskaya, 1957), implying adaptation

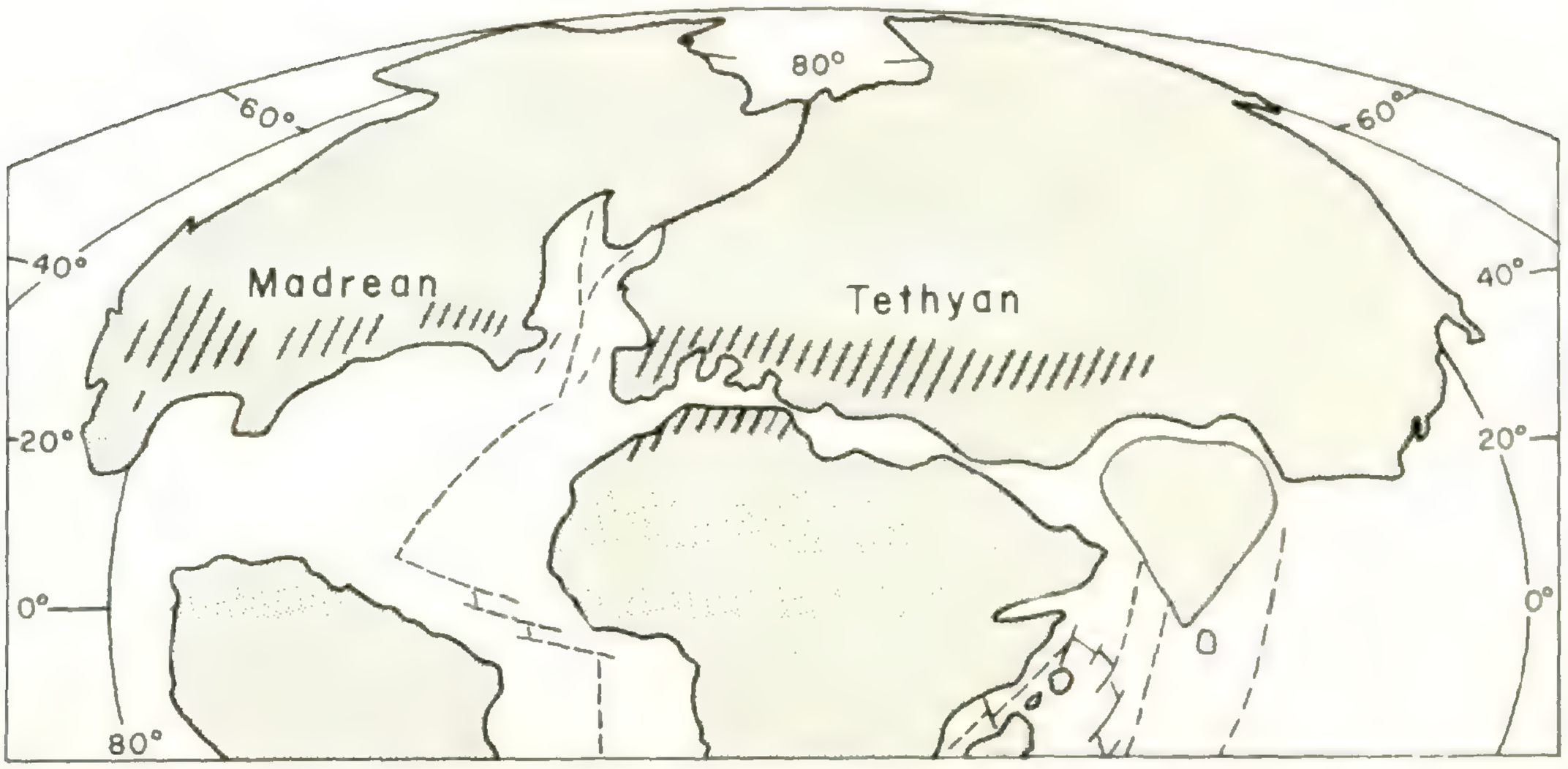


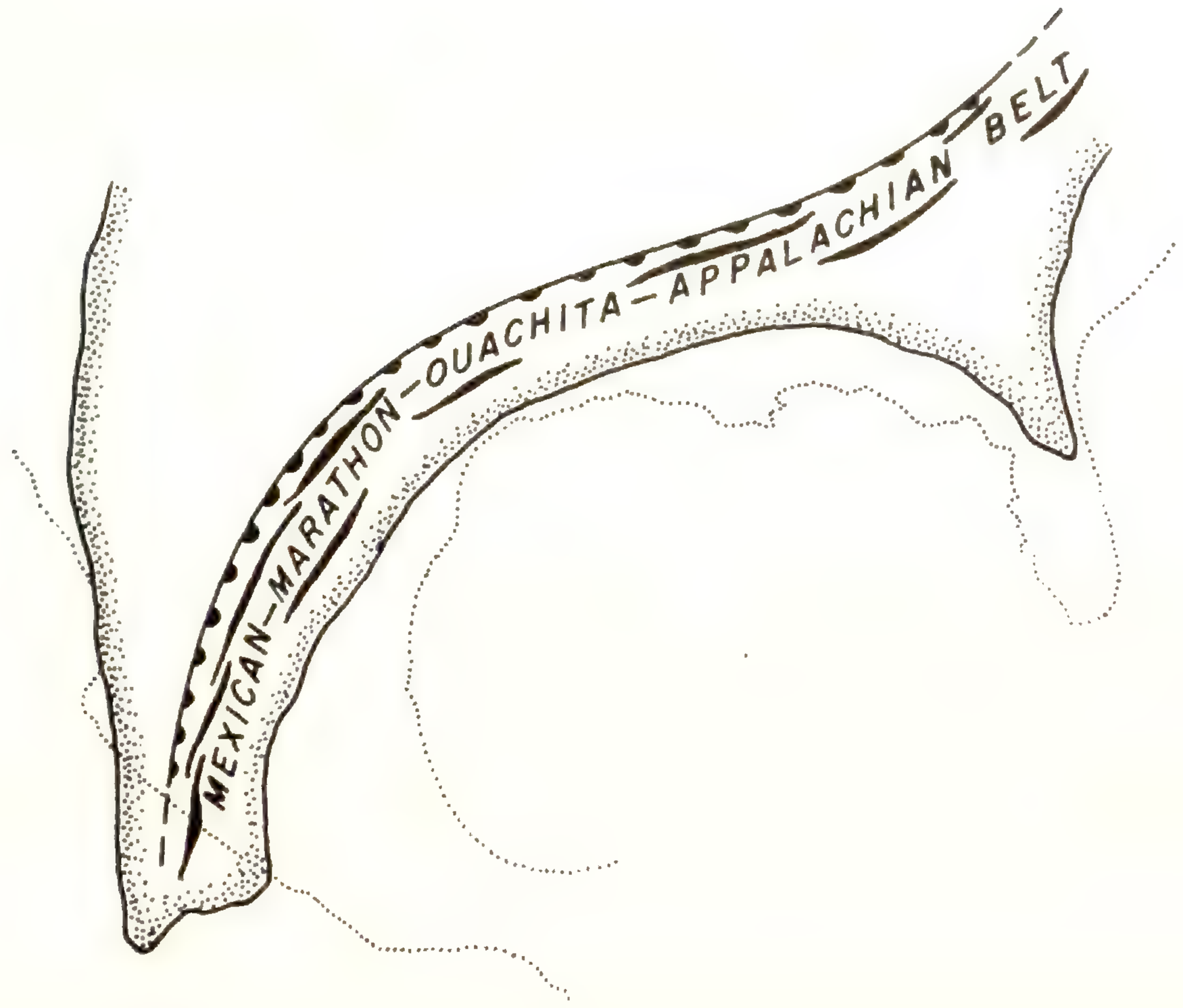
FIGURE 1. Early Tertiary positions of the continents and areas (hachured) potentially occupied by Madrean-Tethyan sclerophyllous vegetation (marine embayments, not shown). Somewhat modified (*i.e.*, India) from Dietz & Holden (1970). For other reconstructions, see Phillips & Forsyth (1972) and Briden *et al.* (1974).

to a climate of much sunshine, moderate (subhumid) summer precipitation, and high evaporation.

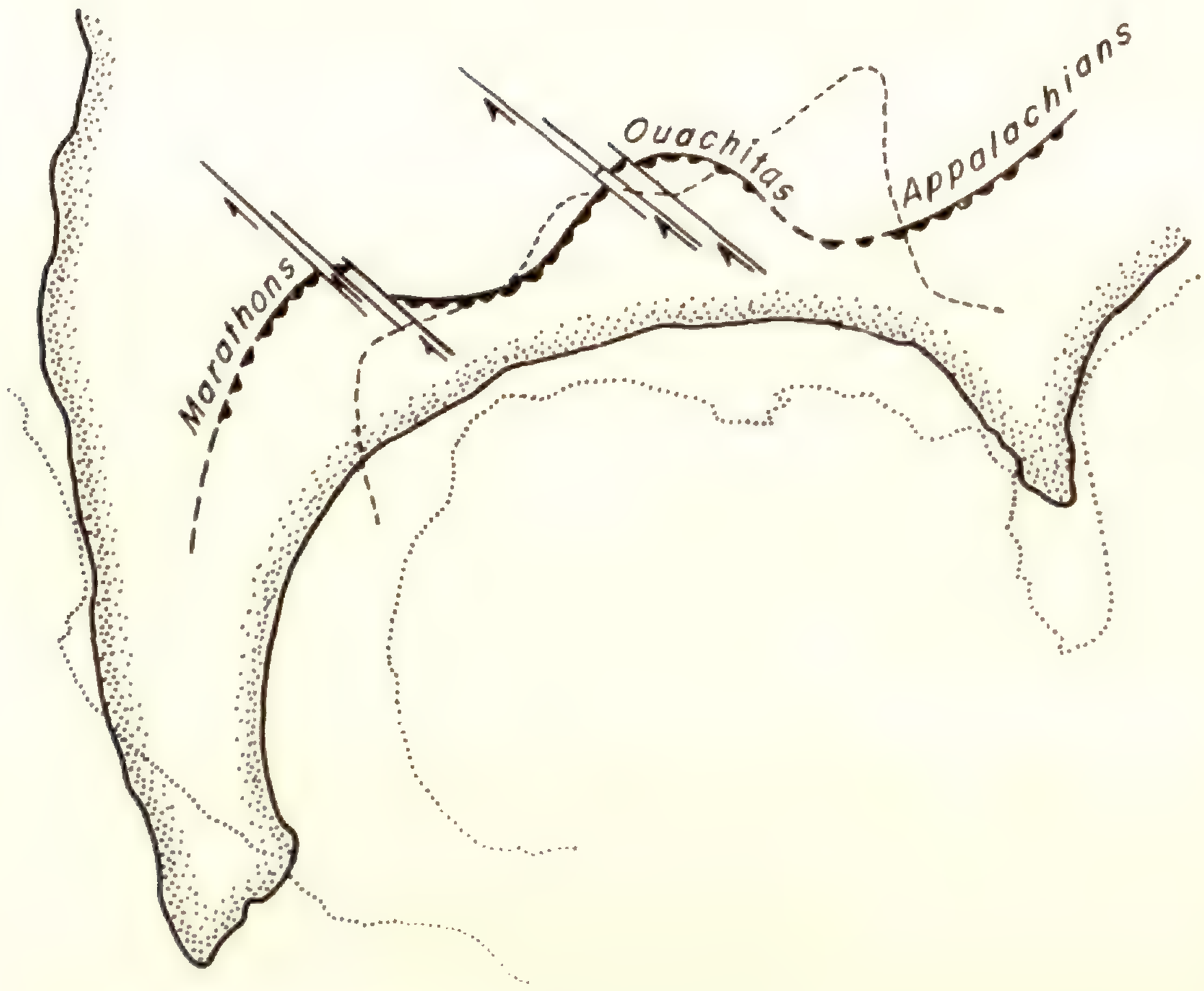
The potential for migration across this region may be inferred from the occurrence today on the granite-gneiss domes of the Piedmont and in the "Fall Line Sand Hills" at the edge of the Piedmont of some 200 taxa, few of which are found elsewhere in the eastern United States. McVaugh (1943) reviewed these distributions and emphasized that many of them find their affinities in the Mississippi Valley, the Ozarks, or in the western United States and Mexico. He draws an analogy (p. 140) between their distribution and that of the black oaks which also have few species in the moister, colder Blue Ridge, but many in the Piedmont-inner Coastal Plain, the Ozarks and southwestern North America. The plants in these edaphically dry areas, both perennials and annuals, include *Agave*, *Forestiera*, *Eriogonum*, *Hedyotis*, *Lotus*, *Oenothera*, *Portulaca*, *Schoenolirion*, *Sedum*, *Talinum*, *Trifolium* and *Yucca*. Other species in the southeastern United States that are rare and not restricted to the granite-gneiss domes are isolated representatives of genera typical of the west, distributed in *Aristida*, *Brickellia*, *Astragalus*, *Cnidoscolus*, *Eriogonum*, *Eryngium*, *Gilia*, *Krameria*, *Muhlenbergia*, *Nolina*, *Opuntia*, *Penstemon*, *Stillingia*, *Stipa* and *Xerophyllum*. Many of them are in the "Fall Line Sandhills" which form a narrow belt at the edge of the Piedmont. The "shale barrens flora" farther north (West Virginia-Pennsylvania) and higher up in the Appalachians shows a similar floristic content (Keener, 1970), though it is not so rich inasmuch as it is in a colder region. Species of *Eriogonum*, *Oenothera* and *Phlox* are attributed to a southwestern source.

McVaugh (1943) concluded that since a large proportion of these xeric species either have the greater parts of their ranges south and west of the Piedmont, or belong to genera that are best developed in the southwestern United States and the highlands of Mexico, they probably were derived from those semi-arid regions.

A


MARATHON-OUACHITA-APPALACHIAN BELT
MEXICAN-MA

B


Marathons
Ouachitas
Appalachians

As he notes, these are not recent distributions for some of the genera are monotypic and confined to the granitic-gneiss domes (*Diamorpha* and *Amphianthus*) and other taxa are represented there by unique, isolated species in their respective genera, notably in *Isoetes*, *Juncus*, *Agrostis*, *Talinum* and *Sedum*. The distinctness of many of the eastern Piedmont species suggests invasion probably occurred in the Tertiary, as does the relict occurrence of some, notably *Sageretia* in xeric coastal sites of Carolina (see Tables 2, 3), or the discontinuous occurrence of clusters of *Helianthemum* species (Table 3) in each area which have diverged since migration.

The evidence reviewed above indicates subhumid climate probably formed a more or less continuous belt across the entire region into the later Paleogene prior to the counter-clockwise rotation of the Appalachian axis (and North America) to its more northerly bearing (Fig. 2). At that time, dry sites may have supported ancestral species of the sclerophylls now discontinuous between southern Eurasia and North America (*Arbutus*, *Juniperus*, *Cupressus*, *Bumelia*, *Pistacia*, *Quercus*, etc.). In this regard, Gray (1960*b*) notes pollen of *Ephedra* is sufficiently abundant in the late middle Eocene Claiborne Formation of Alabama to suggest that it probably was derived from shrubs on local drier sites nearby. She suggests beach dunes near the coast, though *Ephedra* may also have inhabited xeric edaphic sites in the foothill belt to the north. Of the pollen genera listed by Gray, species of the following now contribute to sclerophyllous vegetation: *Celtis*, *Ilex*, *Juglans*, *Ficus*, *Myrica*, Myrtaceae, *Ocotea*, Palmae, *Quercus* and *Sapindus*. Several of these, as well as possible grains of Ericaceae, are recorded from the Claiborne of Hot Springs County, Arkansas (Saunders *et al.*, 1974). Clearly, a search of the pollen record may disclose other sclerophylls of subhumid requirements inhabited the region. According to the thesis adopted here, these would be Tethyan or Madrean in distribution at present.

In regard to dry sites in the region, the Middle Miocene Calvert flora of Virginia and the District of Columbia (Hollick, 1904; Berry, 1909, 1916*a*) provides additional critical evidence. Most of the leaves are very small (nanophyll to leptophyll) and a number of them are entire and coriaceous as well—features indicative of dry conditions. These fossils are so poorly illustrated that the specimens must be examined before the determinations of Hollick and Berry can be accepted. Nonetheless, both of them recognized affinities with plants in the Southwest. In this regard, the legumes have very small leaflets and appear to represent several genera, possibly *Diphysa*, *Caesalpinia* and *Leucaena*. Other taxa include evergreen oaks, a possible sumac, a probable *Ceanothus* (Berry's

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FIGURE 2. Walper & Rowett (1972) propose: A. The Appalachian-Mexican folded belt trended north-south during Late Paleozoic time. B. The Gulf of Mexico owes to separation of the American plates in the Permo-Triassic transition; in conjunction with the formation of the Caribbean, the opening of a sphenochasm produced the Mississippi embayment; accompanying large left-lateral displacement shifted segments of the eastern mobile belt to their present positions. Prior to counter-clockwise rotation of North America following the Eocene, larger areas of exposed dry slopes faced south for occupation by xerophyllous plants in these displaced segments.

Phyllites), and a presumed *Ilex*. Equally notable, there is no evidence here for a rich mixed mesophytic forest. Although some of the taxa are referred to *Ulmus*, *Berchemia* and *Pieris*, their very small leaves remove them from any relation with typical members of those genera; others are very fragmentary. In discussing the assemblages, Berry noted the flora from Richmond, Virginia suggests a low coastal area boredered by cypress swamps. But that at Good Hope Hill, District of Columbia, has small-leaved oaks, *Ilex*, *Vaccinium*, numerous legumes and *Ceanothus*? (*Phyllites*)—all suggesting a region of dry edaphic conditions, possibly coastal dunes. This clearly implies that drier rocky sites at the Fall Line, situated only a few miles west, probably supported a xeric flora.

Evidence of a drier climate in the early and middle Miocene is also provided by the rich vertebrate faunas of northern Florida (Goin, 1958; Olsen, 1962; Estes, 1963; Puri & Vernon, 1964). Some of the fossil mammals (kangaroo rat, badger) indicate relatively dry open country. However, the sedentary herpetofauna probably provides a better indication of environment than the more rapidly evolving mammals. In discussing the origin of the herpetofauna, Goin (1958) assigns a number of taxa to Southwestern and Mexican sources, including a large percentage of big snakes and numerous lizards. He also emphasizes that *Scaphiopus*, a toad of desert affinities, has been in Florida since the middle Miocene (17 m.y.). Although it has lived there continuously in a region where there are abundant ponds, lakes and streams, it has retained its habit of breeding only in temporary water. The tadpoles transform at rates that indicate drying puddles, implying that its breeding habits have remained basically unchanged since the Miocene, though it has been isolated from arid regions where this habit is obligatory for at least 12–13 m.y. Since some of the taxa (*i.e.*, kangaroo rat, badger, desert toad, tortoise) indicate dry sites, it appears that northern Florida as well as lowland areas north to Maryland were essentially a dry savanna-prairie region, which is consistent with the presence of large browzers and grazers in the mammalian faunas, including antelopes, horses, rhinocerotids, camelids and others.

The biologic evidence of dry climate is consistent with that provided by geologic and marine paleontologic evidence. Alt (1974) has noted that high level gravels of the southeastern United States, aligned along the Orangeburg scarp reaching from Virginia south to the Trail-Lake Wales Ridge in central Florida, appear to be remnants of coalescing alluvial fans laid down chiefly by braided streams on a pediplain surface during middle Miocene under dry climate. Deposition of montmorillonite-sepiolite-attapulgite clay minerals in the contemporaneous Hawthorn Formation is consistent with an arid source area. In addition, phosphate deposits in the Hawthorn are considered the result of upwelling of deep, cold waters along the shelf edge of the east coast during the Miocene.

Gibson's (1967) study of the paleoenvironment of the phosphatic marine strata of North Carolina in the Pungo River Formation (a lateral equivalent of the Calvert), and in the Yorktown Formation which overlies the Pungo River unconformably, was interpreted primarily from planktonic foraminifera. Two very different temperature regimes are indicated for the region during deposition. The Pungo River (age = *Globogerinatella insueta* zone, or 22–23 m.y.: see Bandy &

Ingle, 1970: fig. 4) and the lower part of the Yorktown (age = *Globorotalia menardia* zone, or 13 m.y.: see Bandy & Ingle, 1970: fig. 4) contain a cool water benthonic fauna and a dominantly cool water planktonic fauna, both quite different in composition from synchronous subtropical faunas in Florida. During late Yorktown deposition, the benthonic faunas become warm temperate to almost subtropical and have many species that are also in Florida at that time. The faunal relations thus indicate the pre-late Yorktown hydrographic regime was different from the present one, with warm currents situated farther south and with a circulation pattern similar to the present appearing only late during Yorktown deposition (~ 13 m.y.).

To explain these features, as well as those along the entire coastal strip that call for dry climate, Alt (1974) proposed that if the prevailing westerlies dominated over the southeastern states during the Miocene, the entire paleogeographic assemblage (phosphate deposition, diatomites, clay minerals, relict pediplains, paleoclimatic indications) could have a common cause. This would be possible if the continent had relatively low relief, as is now known to have been the case; the western cordillera was elevated appreciably only in the later Tertiary and Quaternary. Coupled with warmer oceans in the west, the principal atmospheric pressure systems would not be so strong as those of today, and the westerlies might well flow east across the continent, bringing a drier climate to the east coast (see Willett & Saunders, 1959: 199–204).

The sclerophyllous taxa of subhumid requirements that are now discontinuous between the subhumid climates of southern Eurasia and North America presumably were eliminated from the Appalachian axis and its western extensions (Ouachita, Marathon Mts.) by spreading colder climates commencing in the late Miocene (post-late Yorktown). In this regard, mild winters typified the western interior well into the Neogene, as shown by the occurrence of *Cedrela*, *Cordia*, *Meliosma* and evergreen oaks in the late Miocene of northwestern Nebraska (MacGinitie, 1962), by *Sabal* in the Pliocene of northern Texas (Chaney & Elias, 1936: 12), and by alligators and other cold-sensitive vertebrates (Hibbard, 1960) and molluscs (Taylor, 1960) in the High Plains well into the later Pliocene.

Fossil and modern floristic evidence not only imply there was east-west migration of sclerophyllous taxa, geologic evidence indicates that it was favored by climate, island stepping-stones, and by continental orientation. The efficacy of migration is demonstrated by the affinities of the modern flora of the Azores. Situated on the mid-Atlantic Ridge 1,000 miles west of Lisbon, it has numerous native Mediterranean taxa that reached there by long-distance transport (Wallace, 1880: 248–253). There also are some endemics in the Azores allied to species in the Mediterranean region. They indicate earlier migrations followed by evolution in isolation, or survival under the insular maritime climate and extermination on the continent. Although trans-Atlantic links between areas of subhumid climate are not numerous today, the occurrence of larger numbers into the Neogene is consistent with migration between the sclerophyllous belts which were at least discontinuous across the area.

Present evidence suggests that interchange across the Madrean-Tethyan region was relatively restricted, inasmuch as comparatively few taxa (so far as now

known) were common to these areas in the Paleogene. This is implied also by the occurrence of distinctive taxa in each region which appear to have originated in their respective areas (Raven, 1973). Thus the Californian sector has *Adenostema*, *Arctostaphylos*, *Carpinteria*, *Ceanothus*, *Cercocarpus*, *Cneoridium*, *Dendromecon*, *Fremontodendron*, *Garrya*, *Lyonothamnus* and *Simmondsia*, most of which range into summer-rain areas to the south and east. In like manner, the Tethyan area is distinguished by its *Ceratonia*, *Olea*, *Chamerops*, *Laurus*, *Myrtus* and *Phillyrea* that are typical of woodland and macchia vegetation and also extend into summer rain areas to the east. A further indication of the distinctness of the floras during much of the past is provided by the live oaks that are so numerous in each area. They are not closely related, but belong to different sections and tribes. Presumed similarities, such as the older grouping of *Quercus chrysolepis*, *Q. virginiana* and *Q. ilex* into Sect. *Ilex*, are the result of homoplasy—not close genetic relationship. Similarly, each area has "closed-cone pines," yet they are now known to represent very different sections (Critchfield & Little, 1966; Little & Critchfield, 1969). The distribution of Tertiary pines and oaks that required subhumid climate may have been restricted chiefly by the problem of transport across water barriers.

Although the preceding data appear to clarify the much-discussed relations of sclerophyllous woody taxa that are discontinuous now between the Californian and Mediterranean regions, it must be reemphasized that they make up only a small fraction of the total floras of these regions. There is a tremendous discontinuity and dissimilarity between the Madrean and Tethyan floras, as might be expected in view of their progressively wider separation by water and distance during Tertiary time. Not only are the woody floras quite distinct, the majority of the herbaceous taxa also differ, as cogently reviewed by Raven (1971, 1973). These differences in both the woody and herbaceous floras of the Madrean-Tethyan regions indicate they are relatively ancient, and that the links between them did not involve much long distance dispersal. The closer correspondence of woody taxa between the Madrean-Tethyan regions in Tertiary time stems chiefly from a more favorable climate and terrain for a wider distribution. Later they were eliminated in the mediterranean regions and elsewhere as climate with summer rain contracted, and as drier steppe and desert climates expanded.

The trans-Atlantic links between the Madrean-Tethyan regions were more or less indirect and discontinuous because direct migration of sclerophyllous taxa adapted to subhumid climate was not possible around the North Atlantic. That area was humid and temperate during the Tertiary, supporting mesic conifers and deciduous hardwoods of Arcto-Tertiary alliance. In this regard, many Arcto-Tertiary genera of woody plants common to the Mediterranean and California regions have important roles in sclerophyll-border communities, notably species of *Acer*, *Aesculus*, *Alnus*, *Clematis*, *Cornus*, *Crataegus*, *Fraxinus*, *Juglans*, *Populus*, *Prunus*, *Rosa*, *Rubus*, *Salix*, *Viburnum* and *Vitis*. All of them inhabited moister sites in the ecotone with the sclerophyllous vegetation of the Madrean and Tethyan provinces, but are unrelated historically to the origin of sclerophyllous taxa and vegetation. Many temperate taxa are derivatives of species in Arcto-Tertiary forests that have persisted in the regions of present summer drought by functional adaptation: by shifting into the moistest sites—along streambanks, seepages, and

cool northerly-facing slopes. The species are distinct endemics in most cases, and usually represent different sections of their respective genera, as noted above for the evergreen oaks and the closed-cone pines. This distinctness extends notably to the herbaceous alliances (see Raven, 1971, 1973). Even though there are numerous genera of herbs and forbs common to each region, as in *Achillea*, *Allium*, *Aster*, *Carduus*, *Crepis*, *Delphinium*, *Festuca*, *Filago*, *Galium*, *Geranium*, *Iris*, *Lotus*, *Plantago*, *Poa*, *Rumex*, *Stipa* and many others, the species are only distantly related and frequently belong to distinct tribes or sections of their respective groups, which are characteristically Mediterranean or Californian though some may be Madrean or Tethyan, having a wider distribution. When we turn to family relations we find that some have their chief centers of evolution in the California region, notably Boraginaceae, Cruciferae, Hydrophyllaceae, Onagraceae, and Liliaceae. In the Mediterranean region, the Caryophyllaceae, Leguminosae and Umbelliferae are proportionally more important, and several of the Californian families (Hydrophyllaceae, Polygonaceae, Onagraceae, Polemoniaceae) are not as well represented there. These differences parallel those displayed by taxa in trans-Atlantic forests today. Differentiation across the inner tropics commenced in the Late Cretaceous (Turonian) when Africa and South America finally parted company, and a forest with many common taxa was severed. Since then, related taxa at the level of genera, tribes and families have gradually emerged in each region, and account in large measure for the distinctness of the New and Old World tropical floras. In addition, the elimination of presently Old World taxa from the New World, and of some American taxa from the Old World tropics following the Eocene, accounts also for the increasing floristic differences between the African-Asian and American tropical floras during the Tertiary. In the same way, though in much lesser degree because of its more recent occurrence, the temperate deciduous and conifer-hardwood forests of eastern North America and Europe were rather similar into the late Miocene. As colder climates isolated them in later times, their taxa have continued to differentiate, but the wide floristic differences today result chiefly from the wholesale elimination of American taxa in western Europe during the glacial ages.

Thus, the floristic evidence as now known supports the view that past Madrean-Tethyan connections have been minor but important; the fossil record may be expected to disclose more of them. The long period of separation of these regions of subhumid, warm temperate climate by major climatic and ocean barriers has led to the development of unique sclerophylls in each area, to the formation of unique tribes or sections of "large" genera that still link these regions, and to significant differences in the proportional representation of some families in these areas.

MEXICAN CLOUD-FOREST

The spread of a belt of xerophyllous woodland vegetation over low–middle latitudes following the middle Eocene bears directly on the problem of the age of the disjunct occurrence of numerous "Appalachian" taxa in the mountains of Mexico and central America. These include mesophytic species of *Acer*, *Carpinus*, *Carya*, *Cercis*, *Cornus*, *Fagus*, *Hamamelis*, *Ilex*, *Liquidambar*, *Myrica*, *Nyssa*,

Ostrya, *Prunus* and *Tilia* in Mexico that are identical or closely related to taxa in the eastern United States. The age of the disjunction has been disputed, chiefly because of the absence of a record. Some have favored the early Tertiary (Berry, 1926; Axelrod, 1939, 1950, 1960; Clements, 1936), others the Miocene (Graham, 1972; Martin & Harrell, 1957; Chaney, 1936) and some the Pleistocene (Deevey, 1949; Dressler, 1954; Sharp, 1953).

Recently, Graham (1973) discovered the pollen of temperate genera (*Abies*, *Picea*, *Alnus*, *Celtis*, *Fagus*, *Juglans*, *Myrica*, *Liquidambar*, *Populus* and *Quercus*) in the middle Miocene Paraje Solo Formation near Coatzacoalcos on the coast of Veracruz, Mexico. Hence, he concluded temperate deciduous hardwoods had migrated there from the Appalachian area by the Miocene, or possibly earlier. However, this interpretation does not take into account the fact that whereas these taxa make up deciduous hardwood forests in the Appalachian region today, in Mexico and Central America most of them are subordinate members of forests in which evergreen dicots dominate (Hernandez *et al.*, 1951; Miranda & Sharp, 1950). Clearly, the occurrence of these "Appalachian" deciduous hardwoods in the Mexican and Central American cloud forests is not due to their southward migration and entry into an evergreen forest previously without them, as implied by Graham (1972, 1973) and others as well (*i.e.*, Chaney, 1936; Martin & Harrell, 1957; Braun, 1950).

These temperate rainforests have persisted there in modified form since the early to middle Eocene, at which time they extended northward to central California, Oregon, Wyoming, Colorado, as well as into the Appalachian region. Although deciduous hardwoods are recorded from the Appalachian area (Brown, 1944; Gray, 1960*b*), they dominated forests in the uplands, where climate was cooler (Axelrod, 1965: 164). At low to middle altitudes they were members of a temperate rainforest (or cloud forest) like that now on the eastern escarpment of Mexico, a forest in which evergreens are prominent. This Eocene forest was replaced at altitudes near sea level by the northern fringe of a subtropical forest that lived under a dry winter season during the middle Eocene (Dilcher, 1973).

The Tertiary cloud-forest of the eastern United States lost numerous evergreen dicots and some deciduous hardwoods as colder climate developed during the Tertiary, and especially during the Quaternary when ice sheets reached south to Lat. 37°. The surviving relict forests that are related to those of the Mexican highlands are not solely the "cove forests" of the Appalachians, but the lowland Southern Mixed Hardwood Forest (Quarterman & Keever, 1962; Monk, 1965) that has a few relict evergreens (*Ilex*, *Myrica*, *Persea*, *Quercus* and *Symplocos*) mixed with the deciduous hardwoods. Not only is it more similar in physiognomy to the temperate Mexican rainforests, it lived under a climate of similar warmth (*ET* 58–62), whereas the Appalachian cove forests are in a colder climate (*ET* 54–56), one which in Mexico supports oak-pine or pine forests of different composition. Apart from the few evergreens in the Southern Mixed Hardwood Forest that indicate relations to the south, the bryophytes and ferns of the escarpment-gorge region of the Blue Ridge in North and South Carolina display a strong Mexican affinity (Cooper & Hardin, 1970; Billings & Anderson, 1966). They appear to have survived because the escarpment-gorge area faces south. As a

result, warm moist air moving up the gorge gives increased (and high) orographic precipitation and the mild Gulf air damps temperature extremes. Hence the region has the most equable climate in the southeastern states, as noted earlier (Axelrod, 1967*b*: 27). Thus, some of the groundlayer "tropical" bryophytes and ferns managed to survive the Quaternary cold waves, but few of the evergreens did.

The evidence now available suggests that in the Eocene temperate rainforests dominated by a mixture of evergreen dicots and deciduous hardwoods covered the central United States, extending southward into Central America on highlands along the present axis of the Sierra Madre Occidental. As noted earlier (Axelrod, 1960: 268), high altitudes are not required: all altitudinal thermal zones are narrower under conditions of highly equable climate (Axelrod, 1965, 1968). The taxa that were in the Mexican region have persisted there in scarcely modified form. They spread into the Sierra Madre of eastern Mexico as it was elevated in the late Cenozoic (Schuchert, 1935; Guzman & de Cserna, 1963; de Cserna, 1960), at which time their area in the western Sierra Madre was reduced by spreading dry climate. On this basis, the pollen of deciduous hardwoods recorded from the Miocene of Veracruz (Graham, 1973) did not make up a deciduous forest in Mexico like that of the present Appalachians, nor did species from such a forest migrate south to become associated with broadleaved evergreens. They contributed to a temperate rainforest situated in the mountains farther west, and well above the tropical lowland rainforest that lived at sea level at Coatzacoalcos, an area to which they were transported. Thus, there appears to be no direct evidence for migration of forest species from the Appalachian region into the Sierra Madre Oriental. Rather, the relations seem explicable by the local differentiation and survival as specialized outliers of a forest that extended across North America into later Paleogene time, at least in local areas. The presumed problem of migration between the southeastern United States and northern Mexico thus appears to be non-existent. The Appalachian taxa are disjunct by default: their earlier associates were eliminated from the region by decreasing temperateness of climate.

This analysis may account for the major anomaly in the composition of the modern temperate forests in eastern Asia and eastern North America. The lowlands from central Japan to northern Taiwan, and coastal and southern China south of the Yangtze are covered with a temperate rainforest composed of evergreen dicots and a sprinkling of deciduous hardwoods, captioned Evergreen Broad-leaved Forest by Wang (1961). It has no close counterpart in the eastern United States in areas of similar climate except along the outer coastal strip from central Florida into North Carolina. Inland, areas with slightly colder winters are occupied by the Southern Mixed Hardwood Forest which has fewer evergreens and in which deciduous hardwoods are more frequent (Quarterman & Keever, 1962; Monk, 1965). This forest is clearly ecotonal to the dominantly deciduous forests farther north and to the evergreen forests to the south or coastward, and in this sense may be compared with the Mixed Mesophytic Forest of China (Wang, 1961).

It was decreasing temperateness (see Bailey, 1960, 1964) following the Oligocene that eliminated numerous broadleaved evergreens from the eastern

United States, and left an impoverished, dominantly deciduous hardwood forest over the lowlands there. The climatic differences are especially emphasized when areas of similar effective temperature (*ET*) are compared, as Tokyo and Washington, D.C., or Augusta, Georgia and Kagoshima, Kyushu Island. As shown by Bailey (1966: 193; see also Vahl & Humlum, 1949), Tokyo has 460 hours of the year with temperatures below 32°F (0°C) as compared with 745 hours at Washington, and 568 hours with temperatures above 80°F (26°C) as compared with 1033 at Washington, yet the warmth of climate is very similar in each area (*ET* = 57.5°F or 14.2°C at Tokyo, 57.2°F or 14.0°C at Washington). Other examples of temperateness in areas of similar warmth have been noted elsewhere (Axelrod, 1964: 53–59, 1967*b*: 5–12, 1968: 717–718; Axelrod & Bailey, 1968: 595–599).

CANARIAN LAUREL FOREST

Many of the unique woody plants that make up the laurel forest of the Canary Islands are represented by very similar (or the same) species in Neogene floras scattered from Spain to western Georgia in the southern USSR (Depape, 1922; Bramwell, 1972; Sunding, 1970; Takhtajan, 1969; Kolakovskii, 1964). The notion that the Pliocene species migrated to the Canaries from the Mediterranean, pervades most discussions of their origin. However, this does not account for the fact that during the late Miocene and Pliocene Canarian taxa in the Mediterranean region lived adjacent to forests composed dominantly of conifers and deciduous hardwoods that are not now in the Canaries, but throughout the temperate parts of Holarctica.

The Pliocene floras of southern Europe (see Depape, 1922, 1928) show that members of the Canarian laurel forest lived with, or were close to, members of 3 floristic groups that are no longer in the Mediterranean basin. These include (1) subtropicals (*Buettneria*, *Cinnamomum*, *Celtis*, *Myrsine*, *Raphiolepis*, *Sapindus* and *Sterculia*) that are now in the moister parts of Africa and Asia; (2) temperate conifers and deciduous hardwoods that are now found in eastern North America (*Carya*, *Liquidambar*, *Liriodendron*, *Morus*, *Magnolia*, *Nyssa*, *Robinia*, *Sassafras*, *Taxodium* and *Ulmus*); and (3) temperate alliances that are now chiefly in eastern Asia, with some extending discontinuously to the Colchic region (*Albizzia*, *Carpinus*, *Cercidiphyllum*, *Diospyros*, *Gleditsia*, *Glyptostrobus*, *Juglans*, *Parrotia*, *Ulmus* and *Zelkova*). Members of all these groups live in regions of ample summer rainfall, and imply similar conditions for the Canarian taxa that lived with them in the Mediterranean region into the close of the Tertiary. In addition, each Pliocene flora has species that have persisted in the more temperate parts of southern Europe (*Acer*, *Aesculus*, *Alnus*, *Clematis*, *Cornus*, *Crataegus*, *Fraxinus*, *Populus*, *Ulmus* and *Vitis*), interfingering with Mediterranean sclerophyllous vegetation in moister sites at lower warmer levels, but most of them are not recorded from the Canarian region. Furthermore, a good number of the typical broadleaved sclerophylls of the Mediterranean (*Ceratonia*, *Chamerops*, *Myrtus*, *Nerium* and *Quercus*) are not now members of the Canarian flora. Throughout the Pliocene, taxa of the Canary Island laurel forest were associated with species of these floristic elements in the Mediterranean province. Farther north, Canarian

taxa rapidly decreased and disappeared for climate there was too cold for them as judged from the increasing numbers of deciduous hardwoods and conifers, and from the general absence there of taxa that suggest warm temperate climates (Depape, 1922, 1928; Szafer, 1964).

It has generally been assumed that the taxa of the Canarian laurel forest migrated to the insular region, and that they have survived there under mild marine climate where they are removed from cold. They are confined to the cool fog-belt that shrouds the windward, north side of the islands during summer. This reduces evaporation and fog-drip keeps the soil moist, which also aids in the persistence of these subtropical relicts. The absence of numerous taxa that were their associates into the later Pliocene of the Mediterranean, and now survive chiefly in eastern Asia or eastern North America is understandable in terms of the lack of sufficient summer rain to support them. Nonetheless, the question arises as to how the seeds of laurels (*Apollonias*, *Laurus*, *Ocotea* and *Persea*) were carried there yet none of the numerous species of *Quercus* that were associated with them in the Mediterranean Pliocene—and are still common in the Mediterranean basin—managed to make the trip. Furthermore, many species that were associated with the Canarian taxa in the Mediterranean inhabit moist sites in that region today (*Acer*, *Alnus*, *Crataegus*, *Fraxinus*, *Smilax*, etc.) in areas that are marginally mediterranean in terms of climate, yet they are not in the Canaries either.

The reason why deciduous hardwoods and conifers of Arcto-Tertiary alliance are absent from the Canary Islands is apparent from the composition of the Miocene and Oligocene floras of the Mediterranean region. The Cervera of Spain (Bataller & Depape, 1950), the Majorca from the Balaeric Islands (Arenes & Depape, 1956), and the Sinigallia flora from central Italy (Massalongo & Scarabelli, 1859) are entirely dominated by broadleaved sclerophylls, including forerunners of endemics that now typify the Canarian laurel forest. Equally important, conifers or deciduous hardwoods of temperate requirements are almost totally absent from these floras. They were then situated farther north in central Europe (or at higher altitudes), and appeared in the lowlands of the Mediterranean region only in the late Miocene (Depape, 1928; Arenes & Depape, 1956). This regional distribution of vegetation suggests that the Canarian laurel forest is only a remnant of the rich laurophyllous vegetation that dominated the area from the southern shores of Europe southward into Africa into the late Miocene, following which it was replaced largely by temperate Arcto-Tertiary forests as colder climates developed, and then by sclerophyllous Mediterranean vegetation.

This inference finds support in two lines of evidence. In the first place, the fossil floras that inhabited the broad Saharan region, as based on numerous studies of fossil woods (reviewed by Aubréville, 1970), were composed of dominantly tropical families from Paleocene into Miocene time. Of the 20-odd families so far identified, not one is diagnostic of temperate environments; only one (Fagaceae) has many species (*Quercus*) represented in temperate climates, yet they also range deeply into the subtropics and tropics. The alliances in the Saharan region from Paleocene into the Miocene are mostly related to the present African tropical flora, including taxa in the Annonaceae, Arecaceae (Palmae),

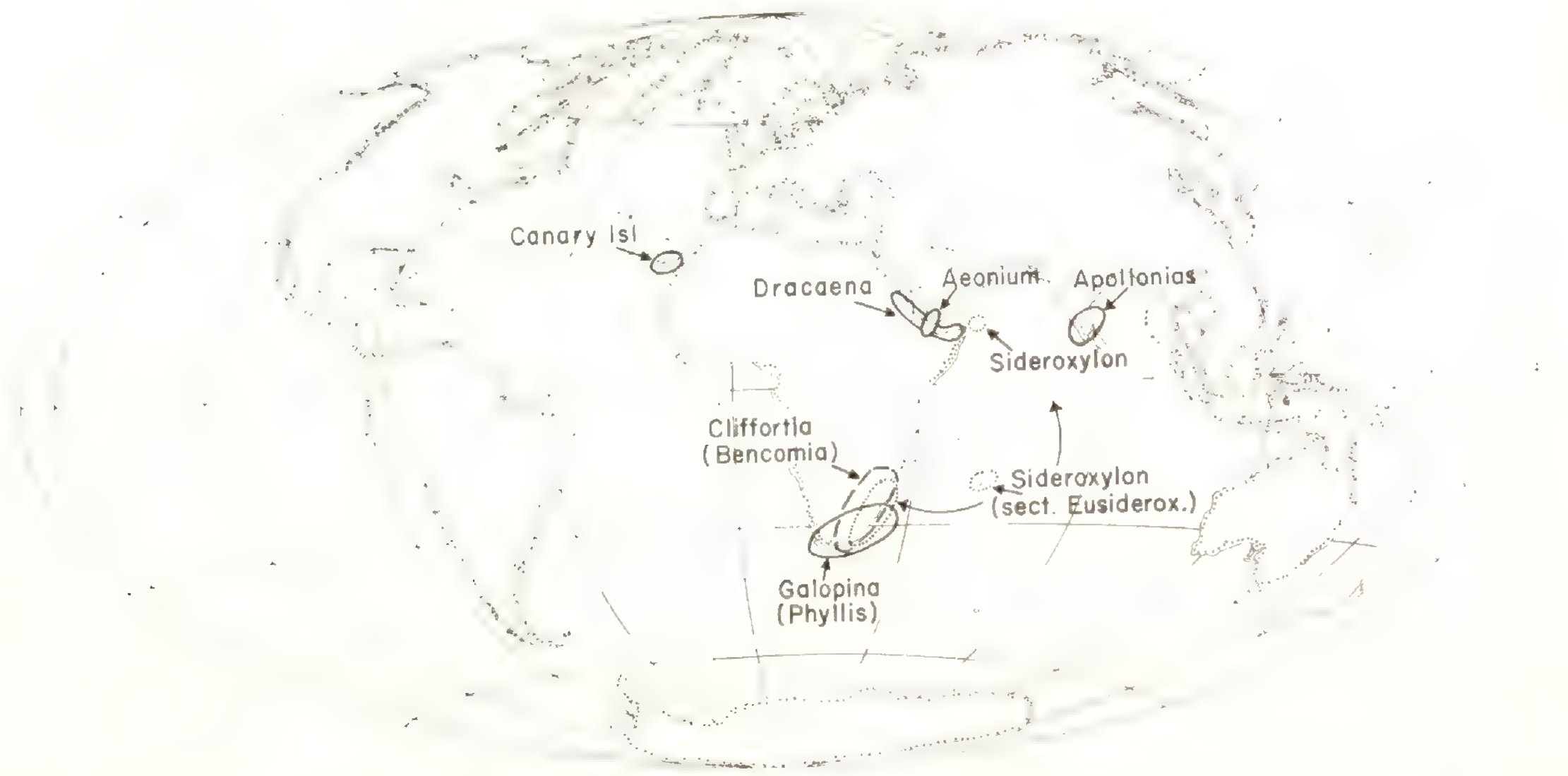

FIGURE 3. Disjunct ranges of some Canarian taxa in eastern Africa and border areas. These may date from the Oligo-Miocene when dry climate commenced to spread across the continent. *Galopina* (Rubiaceae) and *Cliffortia* (Rosaceae) of southeast Africa are related to the Canarian *Phyllis* and *Bencomia*, respectively.

Celastraceae, Combretaceae, Dipterocarpaceae, Ebenaceae, Euphorbiaceae, Hamamelidaceae, Icacinaceae, Lauraceae, Moraceae, Myrtaceae, Proteaceae, Rutaceae, Sapindaceae, Sterculiaceae and Ternstroemiaceae.

The numerous papers of Louvet (1963, 1964, 1965, 1966, 1967, 1968, 1972) and Koeniguer (1966, 1967*a*, 1967*b*, 1967*c*, 1967*d*, 1967*e*) on the fossil woods of Tinehert in the Algerian Sahara near Fort Flatters, at the latitude (28°) of the Canaries, show that from the late Eocene into the Miocene that area supported a tropical flora composed of Combretaceae, Leguminosae and Meliaceae. The Meliaceae woods are similar to *Lovoa* and *Entrandrophragma*, large trees in the dense and humid Guinea-Congonese forest. And *Anogeissuxylon* compares with *Anogeissus* which is found today chiefly in wooded savannas. The woody flora implies alternating savanna and rainforest on the Tinehert plateau in the Oligocene and early Miocene, with palms and numerous woody Leguminosae also present. For the Oligocene, Koeniguer & Louvet (1968) describe *Endandrophragmoxylon* from eastern Fez and near Constantine, implying rainforest along the southern Tethyan shore from Tunis to Egypt. The evidence also indicates a pan-Saharan distribution for *Sterculioxylon* which has been recorded in Rio de Oro, Egypt, Somalia and Libya. Wood of *Dombeyoxylon* also had a wide distribution, including Algeria, southern Morocco, lower Egypt and Syria, implying an environment like that of the living *Dombeya* in the Guinea-Sundanese savannas.

The occurrence of these tropical and subtropical alliances in the present Saharan region into the early Miocene implies laurophyllous forests of the Canary Islands were derived chiefly from the mesic Tertiary rainforests and savannas of Africa proper. This is consistent with the distribution of a number of the Canarian taxa that are found elsewhere only in the eastern tropics (Fig. 3), as noted by Hooker & Ball (1878), by Ceballos & Ortuno (1951: 45), and illustrated by

Bramwell (1972) and Sunding (1970). Among these, *Dracaena* is represented elsewhere by over 150 species in the Paleotropics, yet the Canarian *D. draco* finds is nearest allies in 3 closely related species in Abyssinia, Somalia and Socotra. The pantropical *Sideroxylon* has 100 species, yet the Canarian S. *marmulano* is most nearly allied to taxa in South Africa (Natal), Reunion and Socotra. *Apollonias* has a related species only in southern India (Kerala, Madras). Several other taxa have their nearest relatives only in eastern and southern Africa (Hooker & Ball, 1878: 411; Lems, 1960) though they are not all confined to the laurel forest. These disjunctions are range restrictions in response to the spread of dry climate across northern Africa and southwest Asia following late Oligocene time, a view expressed earlier by Hooker (in Hooker & Ball, 1878: 417): "Finally, the *Dracaena*, together with the tropical trees of *Myrsineae*, *Sapotaceae* (in Madeira), and *Laurineae*, and the Egypto-Arabian types, suggest the hypothesis that at a very remote period these and many other plants of warmer and damper regions flourished in the area included in North-West Africa and its adjacent islands, and that they have been expelled from the continent by altered conditions of climate, but have been preserved in the more equable climate and more protected area of the Atlantic Islands."

The second line of evidence that suggests the Canarian laurel forest was derived from tropical forests of adjacent Africa comes from plate tectonics. Both Africa and Europe moved northward during the Tertiary (Dietz & Holden, 1970; Phillips & Forsyth, 1972), as determined from polar position measured by remnant magnetism in rocks, from the age of the ocean floor, and from lines of volcanos that show direction of movement. In the South Atlantic, the Walvis Ridge and Rio Grande Ridge are lines of volcanoes that erupted from the Walvis thermal center along the mid-Atlantic ridge, and were then transported northward by the moving ocean-floor. Present evidence indicates that in the early Eocene (50 m.y.) the site of the Canaries was near Lat. 18° and moved to its present position at Lat. 28° by the middle Miocene when the African plate collided with southern Europe, Sicily being a piece of Africa (Barberi *et al.*, 1974).

North Africa with the Canarian area has therefore been carried northward out of the tropical zone to a position at its margin. Thus, the Oligocene to middle Miocene floras of north Africa-southern Europe are tropical to subtropical because they were situated farther south, and have moved to their present positions. Hence, the Paleogene trend toward cooling was due at least in part to continental movement, as noted earlier by Hamilton (1968). As for the Canaries, they are composed of two discordant island groups. The low eastern Canaries are continental, but the western volcanic islands are oceanic (Dash & Bosshard, 1969; Rona & Nalwalk, 1970; Dietz & Sproll, 1970). Volcanism that created the western Canaries (Gran Canary, Tenerife, La Palma, etc.) commenced in the middle Miocene (Abdel-Monem *et al.*, 1972) and probably is symptomatic of the continuing deformation of the Atlas Mountains (Kames *et al.*, 1973). These islands no doubt were quickly stocked by laurophyllous trees and shrubs from the bordering continent. This was via the present low eastern Canaries which are continental and were attached then to the mainland as shown by the remains of ratites there (Sauer & Rothe, 1972). Dates of volcanic rocks on Lanzarote and

Fuerteventura (Abdel-Monem *et al.*, 1971) show their ages reach down to the early Miocene (20 m.y.). Thus, it is likely that laurel forests occupied the eastern Canaries by at least this time, invading the western volcanic islands as soon as they appeared in the middle Miocene (16 m.y.). These forests presumably lost numerous taxa as summer rains decreased, as spreading aridity eliminated forests from the low eastern Canaries and from the lowlands of the western volcanic islands, and as colder climates developed during the Pleistocene. Even today cold spells occasionally affect banana plantations over the lowlands. That forests actually inhabited the region is clear from the notice by Schmincke (1968) that stems of bamboo and palm are in the Pliocene rocks of Gran Canary.

It is now evident why the temperate Arcto-Tertiary deciduous hardwoods and conifers that are associated with Canarian laurel forest taxa in the late Miocene and Pliocene in the Mediterranean region are not in the Canaries. The temperate forest did not penetrate southward in the Miocene into lowland Africa, or to the Canarian region, simply because the area was subtropical to tropical. As the African plate moved northward in the Neogene, subtropical laurophyllous forests were carried to the ecotone with Arcto-Tertiary forests, with the latter also having been displaced southward by cooling climate. The Canarian laurel forest is clearly relict to judge from our present understanding of forest history in northern Africa. On this basis, the high percentage of diploids in the flora which reflects antiquity (Bramwell, 1972) becomes understandable, as does the woody habit of much of the flora, the numerous ferns and lianas in it, and the widely disjunct relations of some of its unique taxa. The sclerophyllous evergreen shrubs in it that also contribute to the adjacent macchia further support the opinion that taxa of chaparral and macchia vegetation were derived early in the Tertiary from alliances that contributed to similar laurophyllous forests that were then spread widely across low middle latitudes in both Eurasia and North America.

SUMMARY AND CONCLUSIONS

Broadleaved sclerophyllous taxa that contributed to evergreen woodland and chaparral (or macchia) vegetation occur today in areas with winter rain and summer drought (California, Spain), summer and winter precipitation (Arizona-New Mexico, eastern Mediterranean), summer rain and winter drought (eastern Mexico, northwestern India), and with rainfall rather well distributed through the year (northern coast, Turkey). On each continent, the areas of sclerophyllous vegetation share identical and paired species (or varieties), but are separated now by steppe, grassland and desert climates.

Sclerophyllous taxa entered the fossil record in the middle Eocene, replacing more mesic ones of the earlier dominant laurophyllous forests. The sclerophyllous shrubs and small trees were derived from alliances in laurophyllous forests and many of them contribute to these forests today. Since the adaptive structural features (sclerophylly, small leaves, sprouting habit, deep root system) of chaparral-macchia taxa are also common to related species in mesic laurophyllous forests, they certainly did not originate in response to summer drought, and probably not to pyrogenic conditions. Further perfection of adaptations (sunken stomata, reduced leaf size, thicker leaves, etc.) to drier conditions presumably

took place on lee slopes, in intermontane valleys, and in mineral-deficient sites. Hence, as summer precipitation decreased during the later Tertiary these sclerophylls were preadapted to live in a climate of progressively increasing summer drought.

The basic adaptive structural features of sclerophyllous taxa are therefore not specialized and derived but are ancient and possibly primitive. From an evolutionary standpoint, broadleaved evergreen sclerophylls may best be regarded as "generalists" for they live in diverse environments in which their structural adaptations are rather similar, but in which their functional adaptations adjust as environment changes.

During late Paleocene to early Neogene time, sclerophyllous vegetation extended largely across each continent at low–middle latitudes, inhabiting a broad belt of subhumid climate with summer rain. Many sclerophyllous taxa that are now only in summer-wet areas of the Tethyan and Madrean provinces were formerly in the west, where summer-dry mediterranean climates developed more recently.

The existence of chaparral and macchia over wide areas as "climax" vegetation in the Tertiary seems unlikely. Brushlands were present locally in poor sites ("edaphic climaxes"), and temporarily after natural fires (lightning, volcanism), but they were chiefly seral to oak-pine-laurel woodlands with a rich understory of sclerophyllous shrubs and small trees. Similar communities thrive today in areas where there is summer rainfall like that during the Neogene which then typified the present areas of mediterranean climate.

Chaparral and macchia spread primarily in response to late Pliocene and Quaternary orogenic events which created steep mountain slopes that favored raging fires during the dry season, followed by erosion, soil impoverishment, and the temporary displacement of woodland by shrubland.

The post-glacial Xerothermic period (8,000–4,000 B.P.) greatly favored shrubs in areas previously covered with sclerophyllous woodland, and accounts for some chaparral expansion. However it has been man's destructive activities that resulted in the replacement of sclerophyllous woodland by chaparral today, though most of these are seral potentially.

The present mediterranean climates are therefore not causally related to the origin of chaparral taxa as adaptive types for the taxa are much older than the climate—a condition to which they were preadapted. Functionally, woody taxa adapted simply by shifting germination and seedling establishment into earlier months as the dry season gradually lengthened during the later post-glacial ages.

The history of sclerophyllous vegetation throws light on three biogeographic problems. First, the links between sclerophyllous taxa in North America and southern Eurasia are more numerous when considered in terms of taxa in areas outside of summer-dry mediterranean climates, and when it is recalled that they were more numerous and widespread in the Tertiary. The trans-Atlantic links resulted from east–west migration which was favored by a narrower ocean that had numerous islands, by a more easterly-trending Appalachian axis with scattered dry sites (granite-gneiss domes, shale barrens), and by a more continuous broadly-zoned subhumid climatic belt. There are hints of sclero-

phyllous links in the foothill belt of the Appalachians during Paleogene and Neogene times. Dry edaphic sites in that area still support Madrean taxa that have been there a long time, as judged from their uniqueness. Others presumably were eliminated by the trend to lower temperature, and by the counterclockwise rotation of the continent which eliminated many favorable warm exposures.

Linking sclerophyllous taxa were not abundant because barriers were operative —climate to the north (colder, wetter, longer photoperiod) and water to the east–west—yet they were far more numerous than at present. The Madrean-Tethyan floras are largely distinct today, each region having its unique, autochthonous taxa. As with the sclerophylls, dissimilarity of the herbaceous and perennial floras also implies long separation: if the same genera occur in each region the taxa usually belong to different tribes or sections. This applies also to the temperate Arcto-Tertiary taxa that bordered the Madrean-Tethyan province to the north. Some of them survived in modified form in the Madrean-Tethyan ecotone by shifting functionally to the local, moister and cooler sites within the broadleaved sclerophyll zone.

Second, as Madro-Tertiary woodland spread with expanding dry climate over southwestern North America, temperate rainforests of Mexico-Central America were isolated from those in the western and eastern United States by the middle Oligocene, or possibly earlier. Decreasing summer rain and increasing cold eliminated rainforest taxa in the west, whereas in the East colder winters decimated frost-sensitive evergreen dicots, creating a dominantly deciduous-hardwood forest there. The deciduous hardwoods in the Mexican cloud-forests are therefore relict: they did not migrate there from the Appalachians to enter a forest previously without them, as others have maintained. Elimination of evergreen dicots left a dominantly deciduous hardwood forest in the eastern United States. It finds no counterpart in areas of similar warmth in China-Japan because cold did not so greatly affect that region where forests of similar warmth (*ET*) have more numerous evergreen dicots.

Third, a rich laurophyllous forest ancestral to the present Canarian laurel forest covered much of North Africa and the south shore of Europe into the Middle Miocene. It probably invaded the eastern Canaries in the early Miocene (20 m.y.) and then the western high volcanic islands as they were built up in the middle Miocene (15–16 m.y.). This laurophyllous forest was progressively impoverished as summer rain decreased and as winter temperatures were lowered later in the Cenozoic. It still has several alliances with relatives in the eastern tropics that have survived in this mild fog-belt climate. Thus, taxa of the Canarian laurel forest element in the Late Miocene and Pliocene floras of southern Europe, which were in ecotone with the rich Arcto-Tertiary deciduous hardwood-conifer forest, did not migrate 800 + miles (~ 1300 km) south to give rise to the present Canarian laurel forest, as generally maintained.

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FOSSIL MAMMALS AND EARLY EOCENE NORTH ATLANTIC LAND CONTINUITY

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ABSTRACT

Until recently American vertebrate paleontologists, particularly students of fossil mammals, have not generally accepted the concept of a former continuous land area around the north end of the Atlantic, connecting western Europe with North America. G. G. Simpson developed biological arguments based on fossil mammals supporting the *existence* of a corridor (Simpson, 1953 and references cited there) topologically connecting western Europe with North America in the early Eocene, but Simpson was influenced by the stabilistic geologic rationale of the times when he located the *position* of the corridor in Asia because of supposed permanence of the Atlantic oceanic barrier during all of Tertiary time. He did not take into account the epicontinental Turgai Straits sea barrier in Asia that lay athwart his corridor in the early Tertiary. The plate tectonic geophysical synthesis of the history of the North Atlantic and Arctic Oceans is in accord with the mammalian timing evidence that a former Euramerican landmass as well as a biota was severed about 49 m.y. ago and that Holarctic land dispersal since that time has been via Asia alone, becoming possible again with Europe in the mid-Tertiary. Earlier, starting about 70 m.y. ago, a continental collision whose site is now within northeastern Siberia created land continuity between what were then Asia and North America, and by the Oligocene the Turgai Straits had finally dried, giving the Holarctic corridor essentially its present configuration. Shallow epicontinental waters have on several occasions crossed Beringia, as at present. Thus the land surface of Holarctica has been rearranged substantially since 70 m.y. ago, North America as a land surface having shifted its allegiance from Europe to Asia.

Recently published geological and geophysical information also suggests that, in addition to early Eocene land continuity in the Greenland-Barents Shelf area, a subaerial dispersal route crossing the volcanic Wyville Thompson Ridge from southeastern Greenland to the Faeroes and then to Great Britain and Ireland may also have been possible for a time in the early Tertiary. This latter route is the long familiar but hypothetical Thulean Bridge, now given a new lease on life by geophysical studies of "hot spots."

Aside from the time-honored and romantic concept of Atlantis, a rationale for a former North Atlantic land area connecting western Europe all the way to the North American mainland can be traced back at least to the 1850's. The concept reached a high level of credibility among biogeographers such as Scharff (1907, 1909, 1911) and geologists such as Arldt (1917), and the connection was usually thought of as operating up until rather late in the Cenozoic. It should be recalled that until Nansen's historic voyage in the Fram in 1893–1896 it was generally believed that the Arctic Ocean was shallow and that a significant amount of unknown land still lurked in those waters—land that might somehow have been a terrestrial dispersal route in pre-glacial times. In its extreme form, the idea of a transatlantic late Cenozoic land bridge in the north is still with us (*e.g.*, Strauch, 1970), although the postulated locale is regarded as Iceland rather than farther poleward. On the other hand various authors, for instance Simpson (1953, 1965), Schwarzbach & Pflug (1957), and Schwarzbach (1959), have claimed that no connection between Iceland and the British Isles existed after the Eocene or that none existed at all during the whole Cenozoic Era. Still other authors have sug-

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gested that an Eocene and earlier route was possible in the far north between Greenland and the now mostly submerged Barents Shelf. A few timid souls have hedged their bets by suggesting that both a far northern and an Icelandic route once existed.

Two types of evidence, geological and biological, can be brought to bear on the problem. Before synthesis, these should be kept separate as long as possible in order to avoid circular reasoning. The biological evidence for a biota presumably occupying a former land continuity across the site of the present water barrier connecting the Atlantic with the Arctic Ocean has been discussed with varying results by many authors, either on the basis of low resolution data from distribution of many kinds of present day organisms or on the basis of high resolution data from less numerous and diverse fossils. The low resolution data have naturally given low resolution answers concerning existence, location, and timing, but the high resolution biological data from dated faunas showing high taxonomic resemblance at low taxonomic rank demonstrates that in early Eocene time, about fifty million years ago, a generalized track (Croizat, 1964; Rosen, 1974) for mammals and presumably other terrestrial organisms did exist somewhere between western Europe and North America across the site of the present marine barrier and did not exist to the east of Europe. But exactly where was this track?

Within the last decade both the direct geological evidence for the necessary continuous solid ground substrate for a land continuity and the indirect biological evidence of the biota that must have existed on it before continuity was broken have become less vague. The generalized track has been transformed through new synthesis from a disembodied topology (in the sense of Croizat) to a new geometry. Power of resolution in viewing the subject in all its complexity has increased markedly, so that now rather than dealing with questions of whether and if, we deal in more detail than ever with when, where, and how. Information from vertebrate paleontology, geology, and geophysics has become sufficiently abundant and its analysis sufficiently coherent not only to lend credence to the notion of former continuous land around the north end of the Atlantic Ocean within Cenozoic time, but also to suggest that, although the route was once a major feature of Holarctic paleogeography, continuous land along the entire route cannot have been present after the early Eocene. Although many proponents of North Atlantic land continuity have made the additional conclusion that continuity still existed as late as the end of the Tertiary, the last time that this was the case for the entire route from western Europe across the present northernmost Atlantic to the North American mainland appears instead to have been almost 50 million years ago.

But, until recently, American vertebrate paleontologists, particularly students of fossil mammals, have not generally accepted a North Atlantic land continuity, at least for the duration of the Cenozoic Era. Simpson (*e.g.*, 1953) developed biological arguments on the basis of fossil mammals supporting the *existence somewhere* of a corridor—in other words a land continuity across which high taxonomic resemblance of a relatively balanced biota prevailed from end to end with dispersal occurring in both directions at the same time for various taxa—

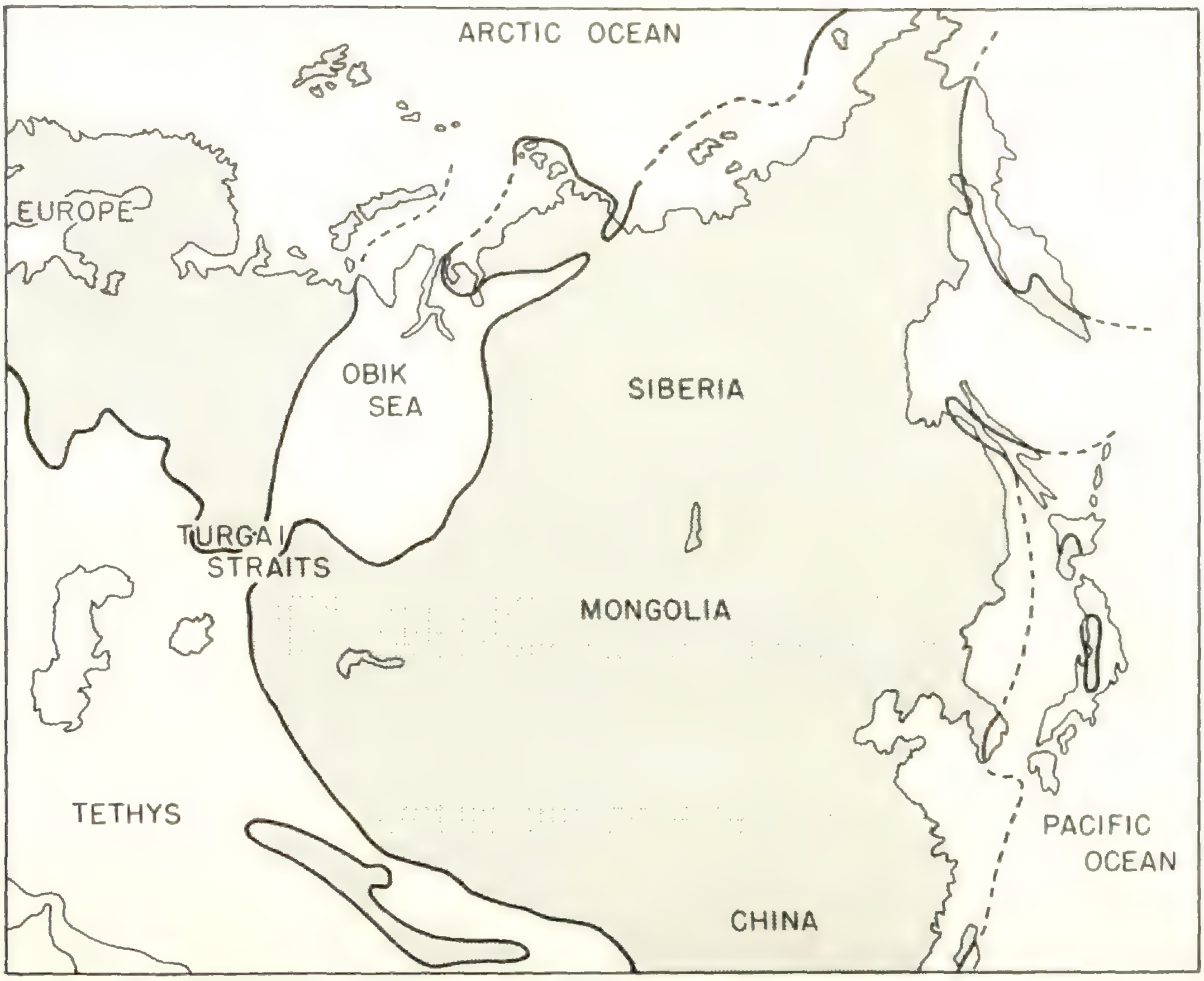

FIGURE 1. Paleogene seaway through the west Siberian lowlands, connecting Tethys to the Arctic Ocean. Based on Zaklinskaya (1970: fig. 47) and differing in detail but not in fundamental features from maps prepared by Sinitsyn (1965) and Dashkevich (1969).

connecting western Europe with North America in the early Eocene (Sparnacian), but he assigned the *position* for the corridor as stretching from western Europe *eastward* to America by way of Asia and Beringia in the same part of the world where continuity indeed existed in the late Cenozoic. The geological rationale prevailing among North American geologists in the 1940's and 1950's was stabilistic, continents and oceans being considered to have had about the same position in the remote past as they have now, so the northernmost Atlantic area was rejected by Simpson and others as a possible early Eocene site for the corridor between North America and western Europe, even though the generalized track for a large number of kinds of early Eocene mammals passed through what is now an oceanic barrier. In addition to the error generated by acceptance of the stabilistic geological model, Simpson did not take into account the epicontinental Turgai Straits marine barrier (Fig. 1), which in the early Tertiary still ran northward from the Tethys Ocean to the Arctic across Asia (Sinitsyn, 1965; Dashkevich, 1969; Zaklinskaya, 1970) and which therefore still prevented continuity of a land biota in that area, thus disrupting Simpson's corridor if its position were postulated to be across that region in the Eocene. Actually, Simpson's biological and statistical evidence for a corridor somewhere at an

undefined position is still basically valid, but his synthesis of biological evidence with incorrect geological information was wrong and simply led to an incorrect location of the early Eocene corridor.

Most importantly, the Eocene break-up of a formerly continuous Euramerican terrestrial biota was masked by Simpson's and other vertebrate paleontologists' acceptance of the stabilist model which, because of its incorporation of a permanent Atlantic-Arctic oceanic barrier, denied that there was an early Eocene Euramerican biota to break up in the first place. In what might be termed the pre-plate tectonic geographic model, the concept of Holarctic continuity via Beringia was extended more or less indefinitely into the past, whereas recent geophysical work suggests that not only the long-lasting (apparently Jurassic through late Eocene) Turgai Straits marine barrier but also a now-vanished oceanic barrier that crossed northeastern Siberia until about 70 million years ago (Pitman & Talwani, 1972; Herron *et al.*, 1974) served to break up Holarctic continuity in the late Mesozoic within what is now Asia. Thus the land surface of Holarctica has been rearranged substantially since 70 million years ago, North America as a land surface having shifted its allegiance from Europe to Asia.

The essence of the plate tectonic reconstruction of the late Cretaceous to present-day geological evolution of the north end of the Atlantic Ocean and its connection with the Arctic Ocean is that about 63 million years ago an extension of the North Atlantic began to open by means of ocean floor spreading between Greenland and Norway in addition to continued spreading in the Labrador Sea. Previous to that time, from about 80 to 63 million years ago, the pole of opening for the North Atlantic had been near northern Greenland (Herron *et al.*, 1974: fig. 5), with compression rather than extension taking place beyond that pole. (Poles of opening have to do with Eulerian rotation of rigid plates on the surface of a sphere, not magnetic poles or the earth's pole of rotation.) Spreading ceased altogether in the Labrador Sea about 45 million years ago as calculated from the magnetic anomaly time-scale (Phillips & Forsyth, 1972) or 48 million years ago as calculated by Hyndman (1973) on the basis of age/depth relations. Meanwhile Greenland and Svalbard slid past one another along transform faults in the Spitsbergen Fracture Zone as Greenland and Norway separated. The nature of the Spitsbergen Fracture Zone offset between the Nansen (Gakkel) Ridge and Atka Ridge sections of the northward extending mid-Atlantic/mid-Arctic ridges has been explained by Wilson (1965), Vogt *et al.* (1970), and Pitman & Talwani (1972) as a transform fault system (Fig. 2). In terms of the magnetic anomaly time-scale Greenland and the Barents Shelf (including Svalbard) finally parted company at about the same time that ocean floor spreading in the Labrador Sea ceased. This break in formerly continuous continental crust at the northeastern corner of Greenland is in reasonably close agreement with an abrupt fall-off in similarity at the generic and higher levels between the mammalian faunas of western Europe and North America dated as occurring about 49 million years ago by K-Ar techniques applied to volcanic rocks and glauconites associated with the mammalian fossils. This fall-off, discussed but not fully documented in recent years (Kurtén, 1966; Russell, 1968; Savage, 1971; Hartenberger, 1972), has been

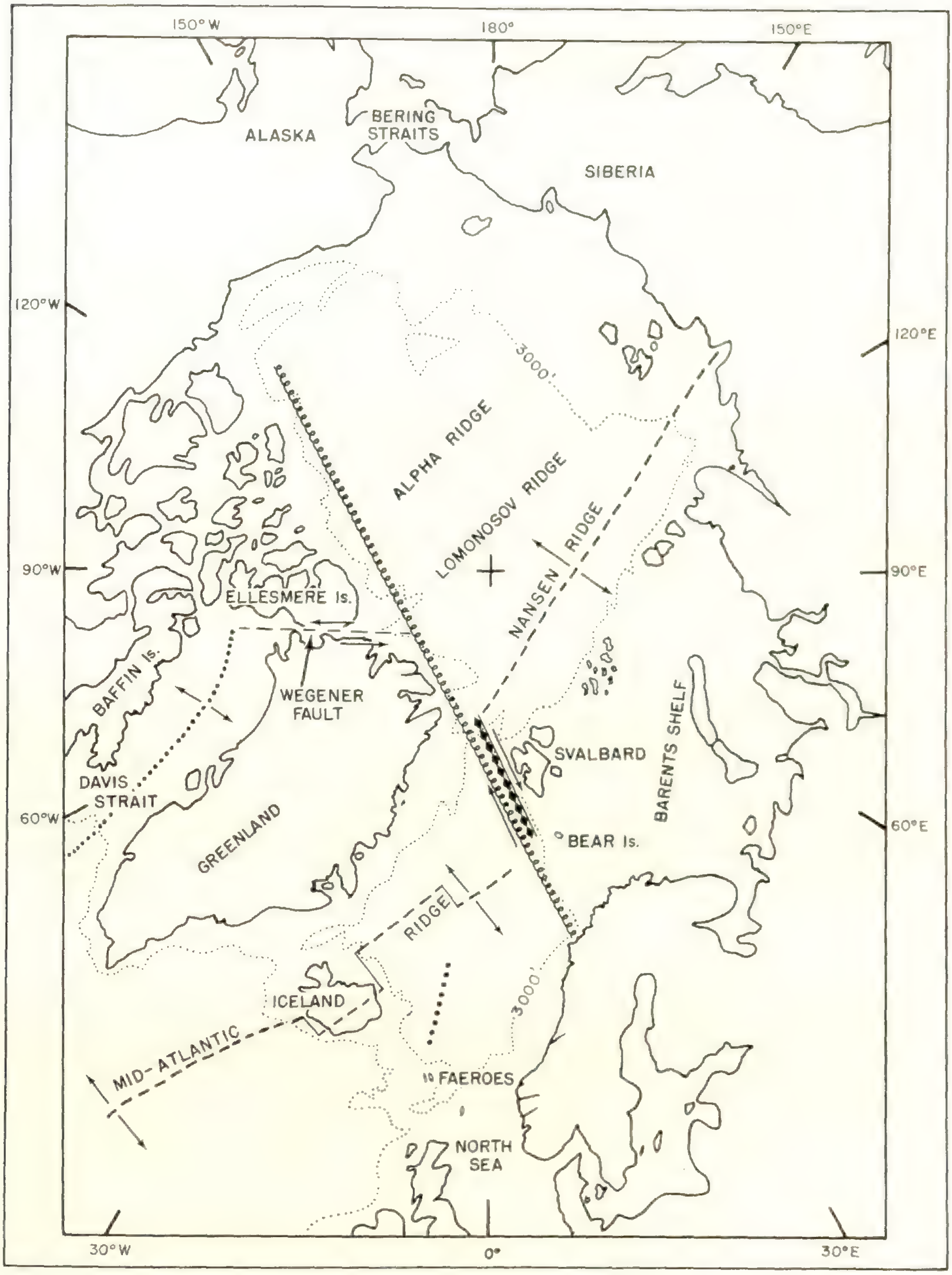

FIGURE 2. Present-day North Atlantic, Greenland and Norwegian seas, and Arctic Ocean, showing De Geer Line (coil) and major transform fault offset of spreading axis along Spitsbergen Fracture Zone (diamonds). Arrows show motion of newly generated oceanic crust. Modified after Wilson (1965).

explained as the natural consequence of final break-up of the land surface of Greenland from Svalbard and a postulated subaerial Barents Shelf (Szalay & McKenna, 1971; McKenna, 1972*a*, 1972*b*) rather than as a result of submergence of some part of a formerly continuously subaerial Brito-Arctic (Thulean Basaltic) Province (Holmes, 1918; Washington, 1922: 780) along a route following the ridge from southeastern Greenland to the Faeroe Islands, then south to Great Britain and Ireland and from there to nearby areas in western Europe.

The driving mechanism for this plate separation has been suggested to be mantle plumes underlying "hot spots" (Wilson, 1963, 1965; Morgan, 1971, 1972; Vogt, 1971; Burke *et al.*, 1973; Schilling, 1973). Recent papers by proponents of plumes revitalize the concept of a formerly subaerial continuity between the northern British Isles and Greenland because they suggest a mechanism for the generation of subaerial aseismic ridges which later sink beneath sea level when ocean spreading has proceeded for a sufficient length of time.

The purpose of this paper is to present and interpret the fossil mammalian evidence concerning an ancient North Atlantic land continuity in somewhat greater detail than I have done previously and to review some recently published information which among other things suggests that, in addition to the eastern part of the De Geer Route (McKenna, 1972*a*, 1972*b*) across the Barents Shelf to Greenland, continuity of the now sundered Brito-Arctic Province between present-day southeastern Greenland and Great Britain and Ireland may indeed have provided an alternate, more southerly land connection from western Europe as far west as Greenland during part of the early Tertiary as various authors such as Schulz (1894) and Gregory (1929) have previously suggested for late Cenozoic time on geologically and geophysically insufficient grounds. Between Greenland and Canada, however, it appears that Davis Strait and Baffin Bay already had become an oceanic barrier by the early Tertiary; for this reason any possible land continuity between Greenland and Canada must have been north of Baffin Bay.

PHYSICAL SETTING FOR CONNECTING ROUTES

The De Geer Route (McKenna, 1971, 1972*a*, 1972*b*; Szalay & McKenna, 1971) in the far north via Svalbard to Greenland and the more southerly Thulean Route (Strauch, 1970) from the British Isles to Greenland have been discussed by many authors but the basis has usually been biogeographic rather than geological. In the following section of the paper I wish to discuss briefly the rudiments of the physical setting for these proposed routes, reviewing information that is either well known, new, or newly interpreted as exploration of the North Atlantic ocean floor has become more complete.

NORTHERN ROUTE

The De Geer Route is simply a result of constructing the pre-drift position of the Barents Shelf, including Svalbard, with regard to Greenland and Ellesmere Island (see Pitman & Talwani, 1972: fig. 8). Presumably, contact of European continental crust with that of North America was maintained for some time after

the start of continental separation in the area because of the nature of the transform fault system represented by the Spitsbergen Fracture Zone. Most of what is believed to have happened in the area results from studies of ocean floor spreading histories of both near and distant areas applied to theoretically rigid plates moving on the surface of a sphere, thus predicting what must have occurred at a distance, but the history of northern Greenland and the Barents Shelf and its islands is now known well enough to contribute its own share of significant information (Wegmann, 1948; Harland, 1969; Orvin, 1940).

The Barents Shelf lies beneath a shallow epicontinental sea stretching from the mainland of Norway northward to Svalbard and Franz Joseph Land and reaching eastward to the twin islands of Novaya Zemlya. A fall in sea level or an uplift of the sea floor of between 250 and 300 m today would result in continuous land from Svalbard to northern mainland Norway either along a more or less direct route following the 40° E meridian or along an indirect route eastward via a high at about 78° N to the 55° E meridian and then south to Novaya Zemlya and the mainland. Between Bear Island and Norway's North Cape, water more than 400 m and locally 500 m deep occupies what appears to be a large drowned drainage system. Smaller apparent drainage systems exist to the west and also to the southeast of Franz Joseph Land.

Nansen (1904) believed that sea level has risen to its present level only since Plio-Pleistocene times. Because he could find no general cause for simultaneous subsidence of diverse coastlines and shelves on the sides of what are now known to be expanding ocean basins, he opted for general changes in sea level to explain the effect. Nansen's value of 400–500 m higher elevation with respect to sea level than today for the Barents Shelf in late Tertiary time and Orvin's (1940) figure of 500 m are based on the concept that the postulated Barents Shelf drainage systems were once subaerial. Either shelf uplift or a sea level drop of 500 m would put the present surface of a continuous Svalbard-mainland land connection at least 200 m above present sea level, to which must be added whatever amount erosion may have reduced that land surface before it was submerged. Preglacial worldwide oceanic volume was somewhat higher, not lower, than at present because of Quaternary water commitment to polar ice caps, but the amount would not be sufficient to drown the Svalbard-mainland connection. The depressing effects of Quaternary ice loading, if any, on the Barents Shelf are unknown. Presumably the Barents Shelf has on occasion stood somewhat higher than at present and is not always an epicontinental marine barrier to terrestrial dispersal.

The present flora of Svalbard has about 160 indigenous vascular plants, of which 120 also occur in northern mainland Scandinavia (Rönning, 1963). About 35 species have high Arctic distribution and do not occur on the mainland. Among the latter are a number of species shared only with Novaya Zemlya (Rönning, 1963: 103). This is compatible with, but of course does not prove, a former direct subaerial connection between these islands via the Barents Shelf. The time of submergence is unknown but could have been in the late Cenozoic.

Lowell (1972) has recently reviewed the structural evolution of the main island of Svalbard, to which the name Spitsbergen has now been restricted. He

found clear evidence of combined right lateral and compressive motion along and parallel to the Spitsbergen Fracture Zone, which has folded and thrust various Precambrian to Mesozoic rocks along the west coast and folded Tertiary sediments in southern Spitsbergen that some workers have thought to be as young as Miocene in age (Flood *et al.*, 1971). Lowell attributed the termination of folding and thrusting to the northwestward departure, beyond the Spitsbergen Fracture Zone, of the continental crust of Greenland, an event which he dated at 15 million years ago on the basis of assumptions that the spreading half-rate north of Iceland has been 1 cm year ^{1}, that such an average has been maintained, that a distance of 300 km of transform motion since the event has taken place, that the compression had to be caused by the pressure of continental crust from across the fracture zone, and that Spitsbergen's continental Tertiary is correctly dated. These assumptions are debatable and are subject to adjustment. Separation of the blocks containing Greenland and Norway from one another at their continental slopes involves about 1000 km over a 63 million year period, or an average spreading half-rate of about 0.8 cm year^{-1}. I estimate a larger minimum transform distance in order for the southern tip of Spitsbergen to clear Greenland than did Lowell: say, 550 km. A 1.6 cm year^{-1} average rate of separation caused by the creation of new crust in the Greenland and Norwegian seas thus would have required at least 34 million years since final contact to produce the present configuration. Any variations in spreading rate might increase or decrease such an estimate substantially.

If indeed rocks as young as Miocene were present in the Spitsbergen Tertiary sequence, Lowell's argument concerning the maximum possible date of folding would receive some slight support; however, the Miocene date harks back to a determination by Heer more than a hundred years ago, made on the basis of long superseded but unfortunately still quoted paleobotanical correlation (Ravn, 1922; Manum, 1962). Present concepts of the age of the entire Tertiary succession have been reviewed thoroughly by Birkenmajer (1972), who concludes as did Ravn and Manum before him that the youngest Tertiary sediments are not younger than about the beginning of the Eocene. Most of the deposits appear to be Danian and Montian, possibly passing upward into Landenian. Compression of Spitsbergen could thus have ceased at any time after about the Landenian insofar as one can tell from biostratigraphic evidence presently known from Spitsbergen.

Pitman & Talwani (1972: fig. 8), on the basis of a reconstruction of plate motions in the Atlantic area made by matching symmetrical isochronous magnetic anomalies and then computing synthetic fracture zones or flow lines, arrived at the conclusion that Spitsbergen and Greenland completed their passage past one another about 47 million years ago. Their evidence is accepted here, although the magnetic time scale on which that date is based may not correspond exactly to the radiometric scale of continental sequences bearing fossil land mammals.

The early Tertiary flora and fauna of Svalbard are well enough known to suggest a cool-temperate climate, in which *Sequoia*, *Ginkgo*, *Cercidophyllum*, and *Ulmus* are represented in addition to numerous conifers including abundant *Metasequoia*. Palms are absent, as well as various warm climate genera such as *Magnolia*, claimed by Heer to be present. Fresh-water mollusca have been

described, as has an amioid fish (Ravn, 1922; Lehman, 1951), but as yet no fossil mammals have been found (Lehmann, 1973).

SOUTHERN ROUTE

Although the De Geer Route is predicted by plate tectonic reconstructions of juxtaposed early Tertiary coasts, a second early Tertiary route across the widening Atlantic Ocean basin may have existed in the Iceland area when the Faeroe-Iceland-Greenland Ridge was created as the result of crustal swelling and simple piling up of excess tholeitic lavas emerging from a proto-Icelandic "hot spot" overlying a major site of mantle upwelling. Increasing evidence suggests that this route was subaerial, but opinions have differed concerning how much of and how long such a route remained available for terrestrial dispersal.

The southeast to northwest trending Faeroe-Iceland-Greenland Ridge is composed of igneous rocks differing in seismic velocity characteristics from both typical oceanic crust and typical continental crust. It was emplaced as Greenland separated from Rockall Bank, the Faeroes, and Norway, starting about 63 million years ago. The ridge is presently aseismic away from Iceland, but it separates areas of ocean floor with quite different spreading histories (Vogt *et al.*, 1970). The ridge is above water along approximately one third of its length at present, at Iceland, and presumably the central accreting part of the ridge has been subaerial much if not all of the time since the inception of spreading by the Icelandic plume or plumes (Burke *et al.*, 1973) at the beginning of the Tertiary. Although until a few years ago it was thought that some of the lavas on present day Iceland could be as old as 50 million years (*e.g.*, Barth, 1941: 8, translated by Dahl, 1963: 187), it has now been determined that the oldest rocks are instead only 12.5 and 16 million years old, respectively, on the southeast and northwest sides of the island (Moorbath *et al.*, 1968). Nevertheless, Iceland can be thought of as a sort of steady state phenomenon constituting a subaerial landmass of about its present size for much longer than 16 million years, any part of the land surface ultimately passing beneath the waves as spreading caused by the creation of new crust carries away that surface either northwestward or southeastward from the central accreting plate boundary that crosses Iceland. About 20 million years would appear to suffice to carry away newly created Icelandic surface to about 200 km in either direction from the plate boundary, which is in general accord with Iceland's subaerial size and with what is known about Atlantic spreading rates at that latitude. Thus the absence of rocks older than about 16 million years on present day Iceland does not mean that there was no subaerial Iceland prior to 16 million years ago; the older, sundered parts of proto-Iceland are now merely off to the sides beneath the ocean's surface and form parts of the aseismic ridge on either side of the present subaerial island.

Although Iceland's actual width as an island above sea level is of course not known or even calculated adequately for various times in the past, its present width would have filled the available width of the Atlantic Ocean about 42 million years ago [(1200–400) (63)/(1200)], assuming constant spreading rates for the sake of argument. Pitman & Talwani's (1972) results indicate greater spreading rates in

the early Tertiary, however, so that 42 million years in this simplified model is too low a figure. Error in the opposite sense is no doubt also introduced because the model does not take thermal relaxation time into account (*e.g.*, Sclater *et al.*, 1971).

Brooks (1973) presented evidence for an enormous Paleocene tholeitic dome overlying a mantle plume or plumes (proto-Iceland), about 200 km in observed diameter and according to him possibly as high as 6 km above sea level, occupying a position near the mouth of Kangerdlugssuaq Fjord in southeastern Greenland, against which the Faeroes would have lain. A convincing fit of Greenland with various European continental fragments has recently been prepared by Vann (1974) and this too places the Faeroes off Kangerdlugssuaq Fjord, taking into account Greenland's continental shelf. As the mantle upwelling causing the plume or plumes carried more and more material from the mantle toward the earth's surface, fissures sundered this dome, initiating plate separation. Brooks (1973: fig. 1) opts for a Y-shaped fracture, with Kangerdlugssuaq Fjord being a failed arm or aulacogen (Burke & Dewey, 1973), and it seems to me that the southern part of the Brito-Arctic Province may also play such a role. Bott *et al.* (1974) demonstrate that continental crust underlies the Paleocene lavas of the Faeroe Islands, which would have been continuous at that time with those of the Kangerdlugssuaq area although they are now situated some 1200 km away. Continental crust is now known to underlie Rockall Plateau as well, but that area was already separated from the British Isles by Rockall trough in the Eocene (Jones *et al.*, 1974). It thus becomes of interest to discover, if possible, when subaerial erosion and subsidence first isolated subaerial proto-Iceland with oceanic waters as Greenland and the Faeroes retreated from the mantle upwelling under Iceland.

Nansen (1904: 74–75, 173–175) seems to have been the first to give topographic evidence of subaerial erosion of the crest of the Faeroe-Iceland-Greenland Ridge, although he explained it by postulating a much lower general sea level in the late Cenozoic. Bott *et al.* (1971), Fleischer (1971), and Vogt (1972*a*) have recently presented detailed geophysical evidence that the part of the ridge that lies between Iceland and the Faeroes was generated by the Icelandic plume or plumes during the Tertiary and stood approximately 2 km higher in the early Tertiary than at present. The deepest parts of its crest are somewhat more than 400 m beneath sea level today. This would have placed the crest well above sea level at the time of its formation, subsequent subsidence having taken place as the result of cooling, following a relaxation curve somewhat like that developed by Sclater *et al.* (1971) although more complex in that Sclater *et al.* were dealing with "normal" oceanic crust uncomplicated by the presence of an aseismic ridge. Vogt (1972*b*) has even suggested that the width of the ridge at any particular place is a function of the rate of magma production by the underlying plume and he therefore concluded that a slowing of ocean floor spreading occurred in the mid-Tertiary because of saddles on either side of Iceland. This would be in accord with the most recent work on magnetic anomalies near the region (Vogt & Avery, 1974). The generally flat top of the ridge from Iceland to the Faeroes, coupled with V-shaped sediment-filled valleys, suggests subaerial erosion followed by

sinking and valley filling as the spreading site over the Icelandic plume pushed the Faeroes away. West of Iceland in Denmark Strait and also at the deepest part of the Faeroe-Shetland Channel (Lightning Channel) identical depths of 583 m mark the lowest points on the crest of the Faeroe-Iceland-Greenland ridge (Huddleston, 1899: 145).

Strauch (1970) believed the final submergence of the Faeroe-Iceland-Greenland Ridge (Thulean Bridge) to have been Plio-Pleistocene in age, mainly on the basis of biological reasoning which I cannot follow. Vogt (1972*a*) believed that the ridge was initially breached perhaps as early as the late Eocene, about 40 million years ago, forming a shallow sill thereafter until about 30 or even 20 million years ago as calculated mainly from the paleomagnetic time scale, after which the depths increased to their present values. Vogt emphasized the effects of Miocene to present-day rapid bottom currents on the eastern flanks of the Reykjanes Ridge and Blake-Bahama Outer Ridge, but I suspect that he underplayed the evidence of similar currents from 45 to 35 million years ago along the east side of the Reykjanes Ridge. Dietz & Holden (1970), Gartner (1970), Calvert (1971), Berggren & Hollister (1971), Berggren & Phillips (1971), Herman (1972), and Weaver & Wise (1974) developed the thesis that the widespread cristobalite-rich, seismically reflective, early to medial Eocene layer known as Horizon A in the North Atlantic and Caribbean is actually the geochemical result of abundant cold Arctic Ocean water reaching the Atlantic via the widening Greenland-Norwegian seas, which would have lowered the carbonate dissolution level. Such water must have crossed the crest of a submerged section of the Faeroe-Iceland-Greenland ridge if the thesis is correct. Although a substantial part of the ridge must have been above sea level, probably a greater prcentage than today because not so much ocean floor had been created, nevertheless breaks in subaerial continuity must have been sufficient by 49 million years ago both to break apart the Euramerican biota in that area and also to encourage the formation of Horizon A. Gibson & Towe (1971) have claimed, however, that a substantial influx of volcanic ash occurred in the Atlantic and Caribbean at about the same time; perhaps both causes acted in concert to produce Horizon A.

The present flora of Iceland has about twelve times as many European as American species (Dahl, 1963: 179). The flora shows subarctic rather than temperate affinities, so Dahl concluded that it cannot be merely a relict of a mid-Tertiary temperate flora but must have dispersed from western Europe to Iceland via a land continuity at least as late as the Pliocene. Dahl would thus break the Thulean Bridge first between Iceland and Greenland, then later to the east of Greenland. The Icelandic fauna shows a similar European flavor (Lindroth, 1957, 1960, 1963). Students most familiar with the Icelandic flora and fauna (see Löve & Löve, 1963, for summaries) seem generally agreed that human agencies have contributed only a minor share to these European similarities. Judged from the geology, however, it would appear that the Faeroe-Iceland-Greenland Ridge had substantial breaks in its subaerial continuity well back in the Tertiary.

Another break in continuity occurs between Greenland and Baffin Island.

Baffin Bay is the former north end of the Atlantic, opening having begun in the Mesozoic. At least in central Baffin Bay, the crust beneath a thick pile of Cretaceous and Cenozoic marine sediments (Martin, 1971) is oceanic (Barrett *et al.*, 1971). Additional rifting is indicated in the early Tertiary by volcanics on either side of the Davis Strait area, dated at about 58 million years (Keen *et al.*, 1972; Clark & Upton, 1971; Vogt, 1971), but no appreciable Cenozoic spreading of the sea floor has occurred in Baffin Bay and no Cenozoic spreading ridge or associated magnetic anomalies have been reported there (Keen *et al.*, 1971). Baffin Bay has been a formidable barrier to land organism dispersal since Mesozoic times; thus, dry-land late Mesozoic and early Cenozoic continuity of Euramerica must have lain north of Baffin Bay if such continuity existed. The effectiveness of Davis Straits as a barrier to the spread of terrestrial faunas has been discussed by Lindroth (1957, 1960, 1963) and its botanical effects have been discussed by many authors. Thus, to the extent caused by latitudinal effects whatever they may have been, the stringency of filtering on dispersal would have been about the same as would have occurred had the entire route been at the paleolatitude of northern Greenland.

MAMMALIAN FOSSIL EVIDENCE

In Table 1 I have attempted to tabulate in rather dogmatic fashion the fossil mammalian faunas of Europe at two different times in the Eocene, interpreted here to have been before and after the final break of the Euramerican biota about 50 million years ago. Endless and fruitless argument could be engaged in over issues such as the question of how much morphologic distance is appropriate for a genus, etc., but I shall simply cut that Gordian knot by listing what seems correct to me at present. Further revisions of Eocene faunas can be expected to modify details, but the main conclusion to be reached from the information given in Table 1 seems secure. I do not list other Tertiary continental faunas because there is no need to; after the medial Eocene, faunal resemblance remained at a low ebb from one side of the Atlantic barrier to the other until the Turgai Straits marine barrier within Asia was broken down at the close of the Eocene. Terrestrial faunal resemblances of western Europe with North America after that time are best interpreted as resulting from dispersal via Asia and Beringia except for a few obvious possibilities such as Arctic foxes and polar bears. For these latter animals we simply do not know the route, although the Bering Route seems most probable.

Eastern Asia's mammal fauna possessed a large endemic element from the Cretaceous to the Oligocene, but this gradually diminished in relative importance as Asian forms dispersed to North America and vice versa. Until the medial Eocene, dry-land dispersal in either direction between Asia and Europe did not occur directly, but took place rather by way of the north end of North America, where dispersal was doubly filtered, once at Beringia and again at northern Greenland. From the beginning of medial Eocene until the beginning of Oligocene time it would appear that Europe was isolated both from Asia and from North America.

TABLE 1. Fossil mammalian faunas of Europe at two different Eocene times.

Sparnacian 54–51 m.y. (France)	Lutetian 49–45 m.y. (France, Germany, Spain)	Overall Distribution				
		A[a]	B[b]	C[c]	D[d]	E[e]
MULTITUBERCULATA						
Parectypodus			×			
Ectypodus			×			
MARSUPIALIA						
Peratherium			×			
	Peratherium			×		
INSECTIVORA						
cf. *Hyracolestes*		×			×	
Didelphodus			×			
Leptacodon			×			
"*Androsorex*"					×	×
"*Dormaalius*"					×	×
Adapisoriculus						×
Palaeosinopa?			×		×	
	Palaeosinopa?			×	×	
geolabidine, indet.			×		×	
amphilemurine, indet.					×	×
	Amphilemur					×
erinaceoid, indet.					×	
mixodectid, indet.					×	
Eochiromys						×
Heterohyus?					×	×
	Heterohyus					×
	Messelina					×
	Leptictidium					×
	Macrocranion					×
	Alsaticopithecus					×
DERMOPTERA?						
Placentidens						×
CHIROPTERA						
Palaeochiropteryx	*Palaeochiropteryx*					×
Archaeonycteris	*Archaeonycteris*					×
	Cecilionycteris					×
	Pseudorhinolophus					×
PRIMATES						
Plesiadapis			×			
Platychoerops						×
plesiadapid, indet.					×	
Navajovius (? = *Berruvius*)			×			
prosimian, indet.					×	
Phenacolemur			×			
Teilhardina			×			
Pelycodus			×			

[a] A, European genus also known from eastern Asia.
[b] B, European genus also known from North America.
[c] C, European genus also known from North America but taxonomic identity could be inherited from previous dispersal.
[d] D, Identification uncertain.
[e] E, Indigenous European genus at the time indicated.

TABLE 1. (continued.)

Sparnacian 54–51 m.y. (France)	Lutetian 49–45 m.y. (France, Germany, Spain)	Overall Distribution A[a]	B[b]	C[c]	D[d]	E[e]
Protoadapis	*Protoadapis*					×
	Caenopithecus					×
	Periconodon					×
	Nannopithex					×
	Arisella?					×
	Pseudoloris					×
	Agerina					×
	Adapis					×
	RODENTIA					
Paramys		×				
	Paramys		×			
Pseudoparamys						×
Microparamys		×				
Reithroparamys		×				
	Aeluravus					×
	Masillamys					×
	Gliravus					×
	Plesiarctomys					×
	theridomyid, indet.			×		×
	CREODONTA					
Oxyaena		×				
Palaeonictis		×				
Tritemnodon		×				
Prototomus		×				
	"Sinopa"		×	×		
Proviverra		×				
	Proviverra		×			
Prodissopsalis	*Prodissopsalis*					×
cf. *Prolimnocyon*		×		×		
	Cynohyaenodon					×
	Creodonta, indet.			×		
	CARNIVORA					
Miacis		×				
	Miacis?		×	×		
Vulpavus?		×		×		
cf. *Viverravus*				×		
Didymictis		×				
miacid, indet.				×		
cf. *Uintacyon*		×		×		
	Cynodictis					×
	CONDYLARTHRA					
arctocyonid, indet.				×		
Landenodon						×
Dissacus		?×	×	×		
	Dissacus				×	
Pachyaena		×	×			
Paschatherium						×
hyopsodontid, indet.				×		
Hyopsodus			×			

TABLE 1. (continued.)

Sparnacian 54–51 m.y. (France)	Lutetian 49–45 m.y. (France, Germany, Spain)	Overall Distribution A[a]	B[b]	C[c]	D[d]	E[e]
Microhyus						×
Phenacodus			×			
	Phenacodus			×		
	Almogaver					×
	Paroxyclaenus?				×	×
	Kopidodon					×
	Pugiodens					×
	PANTODONTA					
Coryphodon		×	×			
	TILLODONTIA					
Esthonyx			×			
	PERISSODACTYLA					
Hyracotherium			×			
	Propalaeotherium	?×			×	
Lophiaspis	*Lophiaspis*					×
Hyrachyus?			×		×	
	Hyrachyus			×		
	Atalonodon					×
	Pachynolophus					×
	Chasmotherium					×
	Lophiodon					×
	Paraplagiolophus					×
	Anchilophus					×
	Palaeotherium					×
	Lophiotherium					×
	palaeotheriid, indet.				×	×
	lophiodontid, indet.				×	×
	ARTIODACTYLA					
Protodichobune			×			
	Protodichobune					×
	Dichobune					×
	Hyperdichobune					×
	Meniscodon					×
	Catodontherium					×
	Choeromorus					×
	Dacrytherium					×
	Tapirulus					×
	Haplobunodon					×
	Mixtotherium					×
	Pseudamphimeryx					×
	Cebochoerus					×
	Rhagatherium					×

Of the 60 Sparnacian mammal genera known from Europe, 34 genera also occurred in North America but only two genera, *Pachyaena* and *Coryphodon*, are known with reasonable probability to have occurred in both Europe and Asia. Three additional genera may have occurred in both Asia and Europe, but their

identification is doubtful for one reason or another. Three of these five genera, including the certainly identified *Pachyaena* and *Coryphodon*, occur abundantly in the North American Sparnacian (Wasatchian) as well. Thus the generalized track for mammals in Sparnacian time did not run eastward from Europe but instead clearly crossed what is now the North Atlantic Ocean.

Perhaps it is appropriate to conclude this review with a quotation taken from A. R. Wallace (1881: 70). Wallace was a proponent of dispersal via land continuity if possible. His ideas contrast with what might be called the Darwinian fascination with theoretical chance dispersal: "Notwithstanding the occasional action of such [chance] causes, we cannot suppose that they have been effective in the dispersal of mammalia as a whole; and whenever we find that a considerable number of the mammals of two countries exhibit distinct marks of relationship, we may be sure that an actual land connection, or, at all events, an approach to within a very few miles of each other, has at one time existed."

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Note Added in Proof

While this review was in press several developments occurred which affect the geological and geophysical arguments discussed. No changes in the text have been made, but future discussants may wish to note the following:

1. Renard & Malod (1974) have presented an excellent summary of the known structure of the Barents Sea. Their references are also useful.

2. Kellogg (1975) has published important new information on the Tertiary of Svalbard that in part conflicts with arguments presented here. Kellogg believes that final separation of Greenland from Svalbard occurred by latest Oligocene or possibly early Miocene time. This seems nearly impossible to me because of the presence of very large-leaved fossil angiosperms in the youngest of the Tertiary sediments (Aspelintoppen Formation).

3. After spectacular initial success, the marine magnetic polarity time scale is in the process of being revised (Tarling, 1975). Marine magnetic anomaly 24, which is the oldest anomaly recognized between Greenland and Norway, may well be as much as 5–8 million years younger than the original estimate of 60 m.y. If true, this will affect all previous arguments based upon magnetic anomaly analysis. Anomaly 24 would then be equal in age or postdate reliable K-Ar dates on Brito-Arctic volcanics preserved on land and would be closer to the final separation date of 49 m.y. based on K-Ar control for fossil mammals.

4. During Leg 38 of the Deep Sea Drilling Project, 1974, two holes were drilled on the flanks of the Wyville Thompson Ridge. One (hole 336) reached what is identified as subaerial basaltic rubble at the edge of the flat top of the ridge northwest of the Faeroes after passing through more than 450 m of marine sediments, the base of which is dated as middle Eocene (Scientific Staff, 1975).

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EVOLUTION AND BIOGEOGRAPHY OF SAXIFRAGACEAE WITH GUIDANCE FROM THEIR RUST PARASITES

D. B. O. Savile[1]

Abstract

A lineage of short-cycled rusts, *Puccinia* species, is recorded on 10 genera and 86 species of Saxifragaceae, including 10 sections and various subsections of *Saxifraga*. These rusts can be arranged approximately in evolutionary sequence. From the rust data it is inferred that Saxifragaceae originated in eastern Asia; migrants radiated early in the Himalayan Region and western North America; a return migrant from North America established *Saxifraga* in or near Japan; migrants from Japan established slightly advanced *Saxifraga* groups in the Himalayas and western North America; migrants from the Himalayas (related to *Melanocentrae*) established moderately advanced *Saxifraga* groups in Europe and North America; finally Himalayan migrants (related to sect. *Kabschia*) established sect. *Trachyphyllum* in Beringia and sects. *Xanthizoon*, *Euaizoonia* and *Porphyrion* in the Alps. These last sections probably evolved during the Pleistocene.

Trying to trace the evolutionary and geographic history of a group of obligate parasites, without consideration of their hosts, must generally be a somewhat sterile pursuit, for the rusts can only follow their hosts wholly or in part. But occasionally a combined study of the two co-evolving groups may be doubly illuminating: first, we have the maximum pool of data to draw upon, so that indications from the parasites may strengthen others derived from the hosts; and, second, the relatively simple morphology of the parasites often allows us to arrange them in evolutionary sequence much more easily than we can do for the hosts, in which flowers and fruit may change rapidly in morphology with altered conditions for pollination and dispersal, and in which habit and leaf form repeatedly reflect altered physical environments. The parasites do, of course, reflect habitat changes to some extent; but their modifications lag behind those of their hosts and are seldom so severe as to be misleading, partly because much of their development is within the stable environment of the host tissues.

This combined approach has proved profitable for Saxifragaceae *sensu stricto*, which harbor an evidently natural group of microcyclic rusts (*i.e.*, devoid of all spore states except telia) in the genus *Puccinia*. Comparative morphology allows us to arrange these rusts approximately in an evolutionary series, following well-tried principles that have been described in several earlier papers (Savile, 1954*b*, 1954*c*, 1968, 1971), for various rust lineages.

Some progress was made in an early treatment of the saxifrage rusts (Savile, 1954*a*) in indicating relative ages of some host genera, sections or subsections. In the next nineteen years the available specimens more than doubled in number; many new host records were obtained; much better geographic coverage was secured; improved familiarity with the plants eliminated some errors in host identity; and the availability of high quality phase-contrast optics allowed much more detailed descriptions of rust spore-wall sculpturings. The revised treatment

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Ann. Missouri Bot. Gard. 62: 354–361. 1975.

(Savile, 1973), which raises the number of rust taxa from 18 to 33, markedly strengthens and expands some earlier suggestions, points to a few necessary redispositions within *Saxifraga*, and allows a more detailed biogeographic projection.

Saxifragaceae, as here conceived, embraces about 20 genera, depending on one's generic concepts, of which *Saxifraga* with well over 300 species is substantially the largest. *Chrysosplenium* and *Heuchera* are moderately large, and the rest grade through *Mitella*, *Tiarella* and *Lithophragma* down to such monotypic genera of Cordilleran North America as *Conimitella*, *Elmera*, *Hemieva*, *Suksdorfia*, *Leptarrhena*, *Peltiphyllum*, *Telesonix* and *Tellima*.

Saxifraga is circumpolar and largely arctic-alpine, with several sections occurring freely in western North America. Most other genera occur wholly or largely in western North America. With abundant recent collecting in Cordilleran North America and the Canadian Arctic, the mycological sampling is now relatively good. We have rust records on 48 species of *Saxifraga*, involving most major sections and on 38 species in nine other genera. Host coverage by any group of parasites is nearly always exasperatingly patchy; and we can view the rust records in Saxifragaceae with some satisfaction, for the approximate relationships of most unrepresented genera or sections are clear from comparative morphology.

The rust records reassure us that the family is natural. A few years ago a colleague expressed doubt that *Chrysosplenium*, centered in central Asia, could be fitted into the family convincingly on morphological grounds. However, *Chrysosplenium* in Eurasia takes two rusts typical of this lineage; and in Yukon *C. wrightii* takes the distinctive *Puccinia austroberingiana*, which also attacks *Mitella*, *Elmera*, *Tellima* and relatively primitive species of *Saxifraga*. In confirmation it may be noted that a Himalayan species, *C. davidianum*, is a relatively tall erect plant with large basal leaves bearing the coarse hairs typical of *Heuchera* and related genera. Thus there seems to be no difficulty in assigning *Chrysosplenium* to the group of genera with parietal placentation, grouped round *Heuchera*, despite its base chromosome number of $x = 12$ rather than $x = 7$.

Morphological adaptations to pollination or seed dispersal supply most generic characters in Saxifragaceae and reflect the principal habitats of the genera. Thus some of the genera may be more closely related than their diverse appearances suggest. Figure 1 shows some dispersal mechanisms found in the family. *Chrysosplenium*, occupying moist forest, wet cliffs or streams, has a flaring erect capsule, which functions as a splash-cup: seeds attached to the wall are thrown out at about 45° from the horizontal by the rebound of a falling water drop. Pollination is at least in part also by splash. *Mitella*, of moist forests, also has a splash-cup, probably independently evolved; but pollination seems to be by mosquitoes or other lower Diptera in the greenish-yellow-flowered species and by higher Diptera in white-flowered species. *Tiarella* has a horizontal capsule with a long lower valve, and the seeds are ejected by a springboard mechanism also powered by the kinetic energy of falling water drops. In primitive species of *Heuchera* the many small capsules are randomly oriented and many seeds must land in the basal rosettes; but in advanced sections we see a spike-like panicle

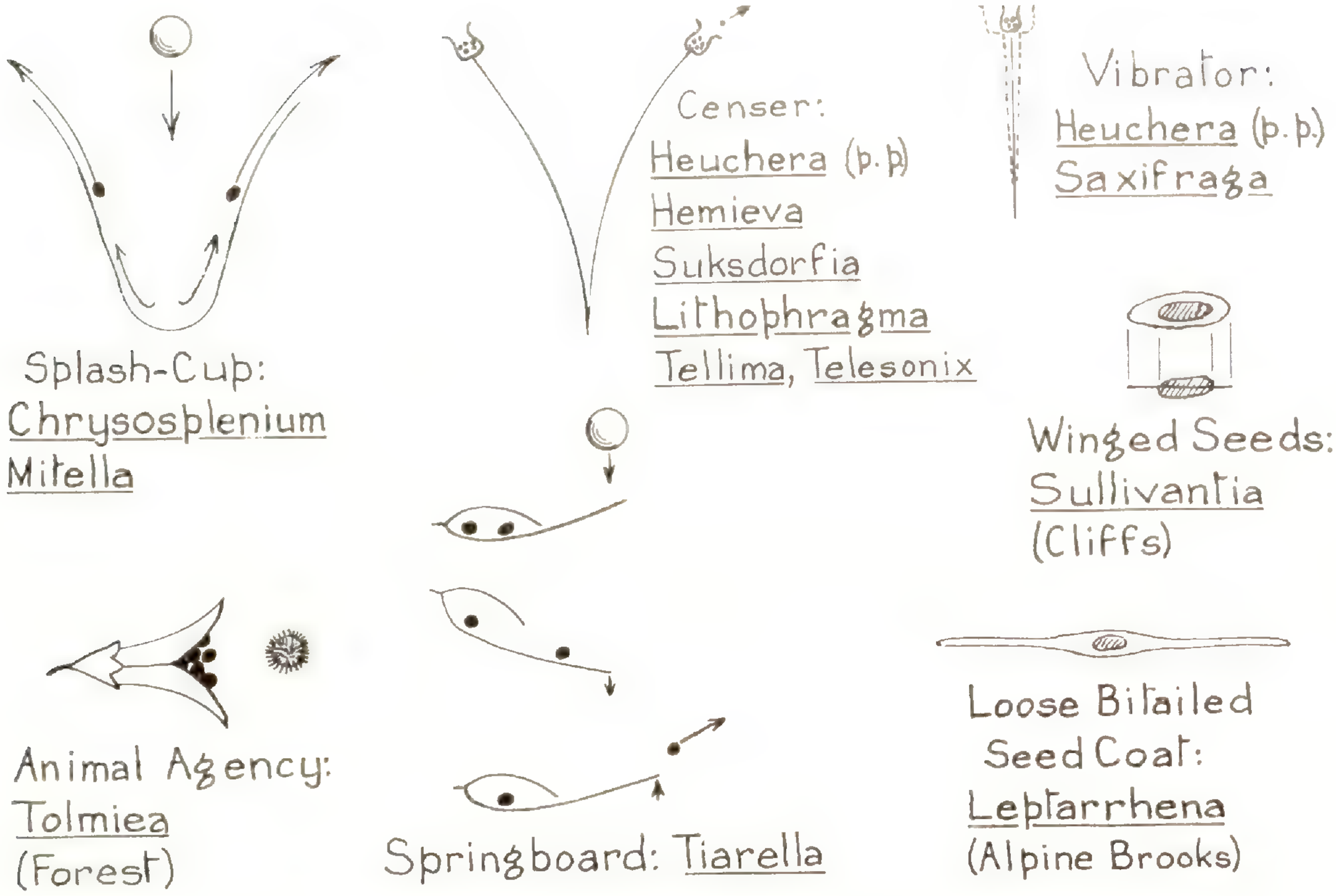

FIGURE 1. Examples of the varied dispersal mechanisms in Saxifragaceae.

with erect capsules, and dispersal is evidently mainly by the censer mechanism, with flexible stems swung by wind or passing animals, but grading into a rigid stem in which high wind speed induces a resonant vibration, bouncing seeds out into the slipstream. The vibrator mechanism reaches perfection in *Saxifraga* (Savile, 1972). *Hemieva*, *Suksdorfia*, *Tellima*, *Telesonix* and *Lithophragma* seem comparable to advanced *Heuchera* in dispersal systems. *Tolmiea*, a forest relative of *Heuchera*, has small but otherwise typical butterfly flowers (yellow and brown, strongly three-dimensional, zygomorphic); and its flaring horizontal capsules expose bristly seeds that must be spread by birds or mammals. *Leptarrhena*, of alpine brook habitats, has small seeds with a loose, strongly bitailed coat that facilitates aerial and aquatic transport (a device that has arisen several times in monocotyledons and dicotyledons). Thus we see that there is marked morphological plasticity in the family.

For the rusts Fig. 2 depicts a slightly condensed summary of the spore types, arranged in approximately a developmental sequence. The upper numbers, in parentheses, are the spore types; those below identify the rust taxa according to the full tabulation in Savile (1973) and the condensed tabulation in Table 1. In type (1) the spores have firm pedicels, always germinate *in situ*, and have smooth walls with conspicuous apical thickening (a protective device). In type (2) the pedicels are delicate and irregularly deciduous, and the apical thickening is considerably reduced, but the spore walls are still normally smooth. In some populations of *Puccinia heucherae* (No. 8) occasional spores show a few very faint striations. In succeeding types the pedicels are freely deciduous, and the

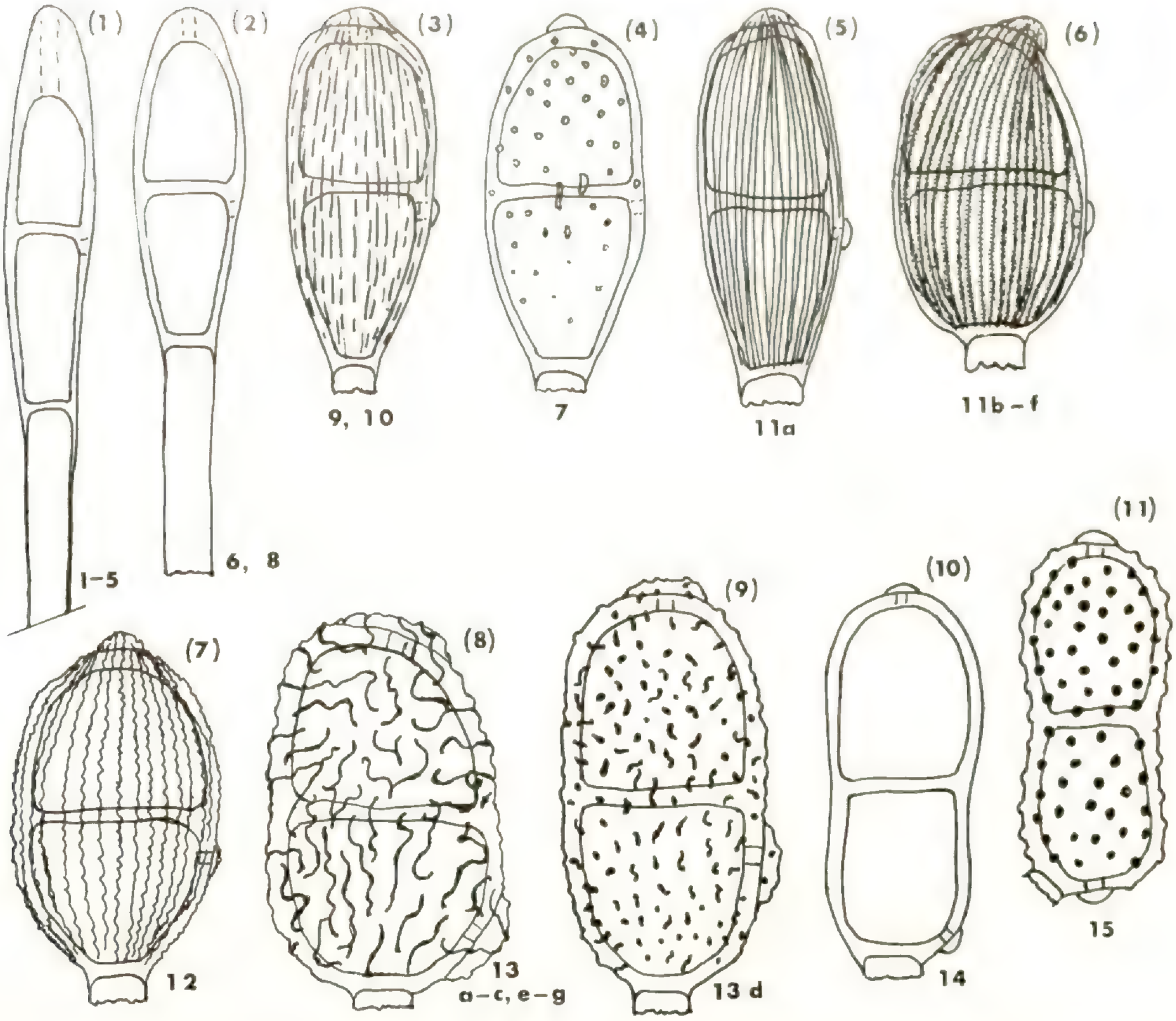

FIGURE 2. Principal spore types in *Puccinia* spp. attacking Saxifragaceae. Upper numbers in parentheses are spore types referred to in text. Open lower numbers and letters are species numbers and varieties of Table 1.

germ-pores have distinct caps. In type (3) the spore walls are faintly striate and in (4) they are faintly verrucose. In type (5) the walls are clearly but smoothly striate, and in (6) they are more coarsely striate, the ridges generally having delicately fimbriate margins (visible only with phase-contrast); and in both these types there is a tendency for the lower germ-pore to be depressed from the ancestral position at the septum. In type (7) the ridges are conspicuously sinuous and are often serrate as seen in side view. In type (8) the ridges are no longer continuous but are irregularly labyrinthiform, and in (9) they are much shortened and tending toward circular warts. In (10) and (11) the lower germ-pores are nearly basal and basal, respectively; but, although the walls in the last type are regularly verrucose, in (10) *Puccinia fischeri*, mainly on *Saxifraga oppositifolia*, the spores are smooth-walled. This rust, unlike all the others, is systemic-perennial in its perennial hosts. Thus, in this species only, there is no need for unfailing yearly dispersal. Survival is ensured by the perennial mycelium; and long-range dispersal occurs when host branches blow across sea-ice or wind-packed snow. Thus the energy-consuming process of ornamentation seems to have

TABLE 1. Hosts and distribution of saxifrage rusts. For detailed host ranges see Saville (1973: table 1).

Rusts (*Puccinia*)	Hosts[a]
1. *P. tottoriensis*	*Mitella*—Japan
2. *P. asiatica*	*Mitella nuda*—E Asia
3. *P. tiarellaecola*	*Tiarella*—Japan
4. *P. saxifragae-ciliatae*	*Bergenia*—montane Himalayas
5. *P. laurentiana*	*Saxifraga nudicaulis*—Bering Sea
6. *P. chrysosplenii*	*Chrysosplenium*—Eurasia
7. *P. harae*	*Chrysosplenium axillare*—Kashmir
8a. *P. heucherae* var. *heucherae*; 8b, var. *meridionalis*; 8c, var. *minor*; 8d, var. *cordillerana*	*Heuchera* (1,2,4), *Mitella, Tiarella, Tolmiea, Saxifraga* sect. *Boraphila* (2)—North America
8f. *P. heucherae* var. *japonica*; 8g, var. *saxifragae-micranthae*	*Saxifraga* sect. *Boraphila* (1)—Japan; S. sect. *Boraphila* (4)—Himalayas
9. *P. saxifragae-gei*	*Saxifraga geum*—Spain
10a. *P. austroberingiana* ssp. *austroberingiana*; 10b, ssp. *saxifragarum*	*Chrysosplenium wrightii, Elmera, Mitella, Tellima, Saxifraga* sect. *Boraphila* (1,2), S. sect. *Diptera*—NE Asia, NW North America
11a. *P. saxifragae* var. *saxifragae*	*Saxifraga* sect. *Boraphila* (4)—Himalayas; S. sect. *Miscopetalum*, S. sect. *Nephrophyllum* (3), S. sect. *Boraphila* (6)—Europe
11b. *P. saxifragae* var. *curtipes*; 11c, var. *longior*; 11d, var. *heucherarum*; 11e, var. *holochloae*; 11f, var. *mitellae*	*Saxifraga* sect. *Nephrophyllum* (4), S. sect. *Boraphila* (3,5,7)—North America & circumpolar; *Heuchera* (2,3,4,5), *Mitella*—North America
12. *P. lithophragmae*	*Lithophragma*—W North America
13b. *P. pazschkei* var. *heterisiae*; 13e, var. *ferrugineae*	*Saxifraga mertensiana, S. ferruginea* —W North America
13c. *P. pazschkei* var. *tricuspidatae*	*Saxifraga* sect. *Trachyphyllum*—Arctic, montane W North America
13d. *P. pazschkei* var. *jueliana*; 13g, var. *oppositifoliae*	*Saxifraga* sect. *Xanthizoon*, S. sect. *Porphyrion*—Arctic, Alps
13a. *P. pazschkei* var. *pazschkei*; 13f, var. *huteri*	*Saxifraga* sect. *Euaizoonia*—Alps only
14. *P. fischeri*	*Saxifraga* sect. *Porphyrion*, S. sect. *Xanthizoon*—Arctic, Alps
15. *P. joerstadii*	*Saxifraga* sect. *Porphyrion*—Alps only

[a] Numbers under *Saxifraga* are subsections of Engler & Irmscher (1916–1919); numbers under *Heuchera* are sections of Rosendahl *et al.* (1936).

been selected against after adoption of the systemic habit. Although types (6)–(11) are plainly more advanced than types (1)–(5), their precise linear sequence is somewhat arbitrary.

With the morphology of the rusts to guide us we may turn to Table 1, which epitomizes the host and geographic ranges of the various rusts. The numbers and letters at the left are the rust species and varieties from Fig. 2 and the taxonomic revision.

Note that we start in eastern Asia, with some excursions into the Himalayas or

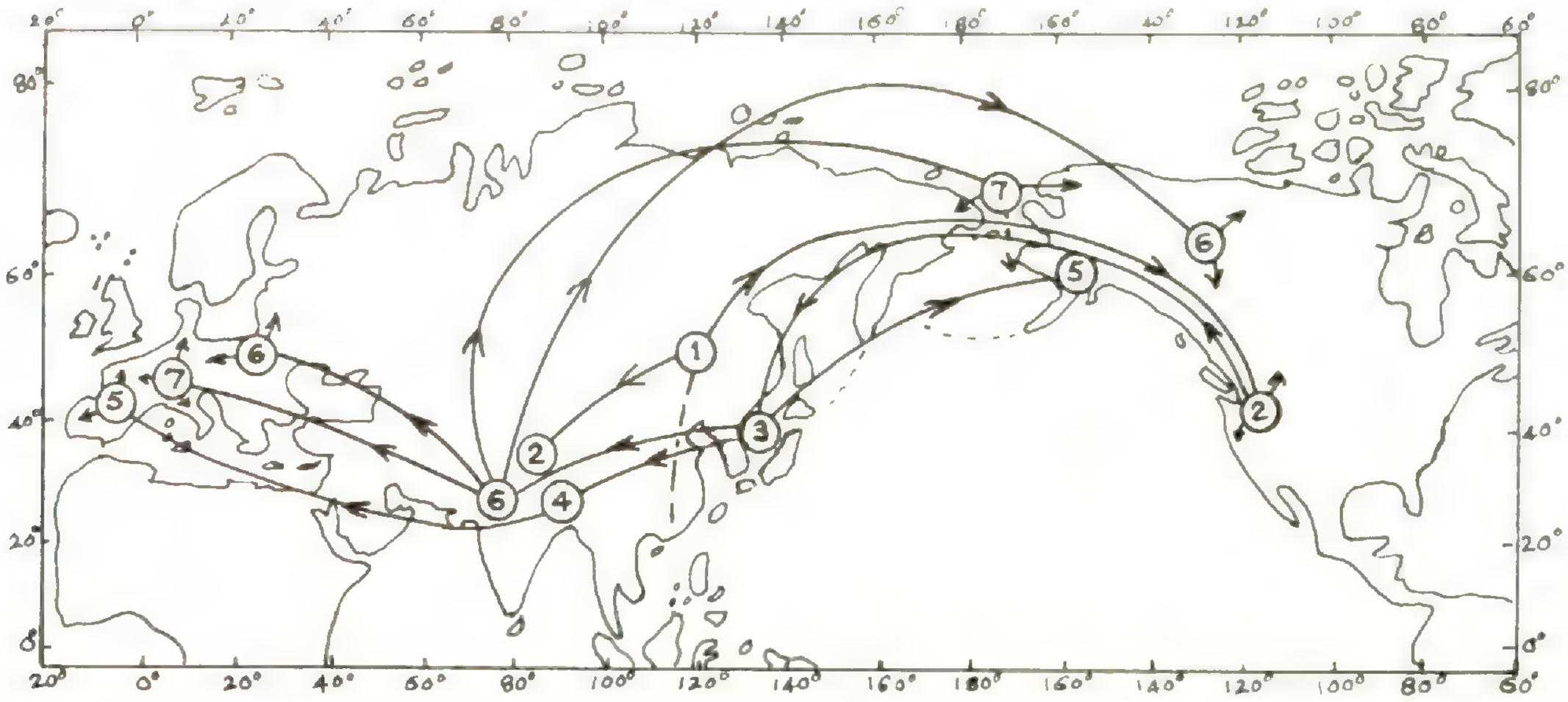

FIGURE 3. Principal dispersions and radiations of early Saxifragaceae and genus *Saxifraga*. Numbers show approximate sequence of radiations.

further. Only with No. 8, the *Puccinia heucherae* complex, do the rusts appear in North America, which thereafter is increasingly important. Coastal and inland races of *Puccinia austroberingiana*, No. 10, are centered on Beringia and reach from Japan to central Keewatin. The most primitive variety of the *Puccinia saxifragae* complex, No. 11, is in the Himalayas and Europe; but the others are either circumpolar and North American or wholly North American. Numbers 12, 13b and 13e are limited to western North America; and 13c is widespread in western North America on *Saxifraga bronchialis* ssp. *austromontana* but also has spread across the Canadian Arctic to West Greenland with *S. tricuspidata*. Numbers 13a, 13f and 15 are restricted to the Alps; and 13d, 13g, and 14 are in both the Alps and the Arctic. Thus it is clear that the most recent radiations in *Saxifraga* and its parasites have been in Cordilleran North America and the Alps.

In Fig. 3 the main migrations of Saxifragaceae are traced on the basis of the evolutionary sequence of their rusts. In this map I have assigned numbers to the radiations that approximately express their relative chronology.

We clearly start in eastern or southeastern Asia with an ancestral plant that may have looked much like *Astilbe*. The first radiation, marked (1) on the map, gave rise to the ancestors of *Tiarella* and *Mitella* in eastern Asia; but probably also sent a branch (2) westward into the Himalayan region that gave rise to *Chrysosplenium*, and another branch (North American 2) crossed the Bering Bridge to give rise, through a more extensive radiation, to the beginnings of various North American genera. Conceivably, *Mitella* and *Tiarella* also started in North America and migrated back to Asia, but their most primitive rusts are on the Asiatic side. One product of this cordilleran radiation must have been a "protosaxifraga", which recrossed the bridge and radiated (3) in or near Japan where the most primitive *Saxifraga* species are found. This complex evidently sent branches to the Himalayan region. The first, which bore a smooth-spored rust (the forerunner of *Puccinia heucherae* var. *saxifragae-micranthae*), perhaps initiated *Boraphila* subsect. *Melanocentrae* (4); and from it at least one radiant reached Europe,

bearing *P. saxifragae-gei* with incipiently striate spores (European 5). A slightly later radiant from Japan entered Beringia, where a radiation (North American 5) gave slightly more advanced *Saxifragae* harboring the faintly but regularly striate *P. austroberingiana*. Another migrant from Japan, bearing presumably ancestral *P. austroberingiana*, later radiated in the Himalayas producing *P. saxifragae* var. *saxifragae* on *Melanocentrae* (Himalayan 6). From this complex a branch reached Europe (6), giving the same rust on moderately advanced *Saxifraga* species; and a later branch reached North America, probably via the Siberian coast, to produce the mainly cordilleran subsect. *Nivali-virginienses* with the rust *P. saxifragae* var. *curtipes*. In North America this rust gave rise to subtly distinct varieties on advanced species of *Mitella* and *Heuchera*. In the meantime *Saxifraga* in the Himalayas was moving into more arid habitats giving rise to sect. *Kabschia*, having over 60 species, with cartilaginous, often spinulose and closely imbricate leaves. *Kabschia*, now extending from Yunnan to the Pyrenees, is not known to harbor any rusts; however, not only do most species grow in mycological terra incognita, but dark rust sori are difficult to see on small imbricate leaves speckled with deep shadows. Probably in *Kabschia* is to be found a rust ancestral to *Puccinia pazschkei* (No. 13 in Table 1). It is fairly certain that radiants from Himalayan *Kabschia* gave rise to sects. *Xanthizoon*, *Euaizoonia* and *Porphyrion* in the Alps and to *Trachyphyllum* in Beringia. These are the radiations marked (7) on the map. *Trachyphyllum* is represented disjunctly in the Alps by S. *aspera*, which probably spread there south of the ice front in one of the Pleistocene glaciations and later was eliminated from lowland areas. Incidentally, petal colours in *Kabschia* range from white through cream to bright yellow, and through pink to deep rose. Thus the group has the genetic potential to give rise to the yellow-flowered *Saxifraga aizoides* and the pink- to magenta-flowered S. *biflora* and S. *oppositifolia*. Some species of the sections that evolved in the Alps have spread into the arctic; but much, at least, of this spread seems to have been Postpleistocene. As already noted, the potential dispersal rate of *Saxifraga* in the arctic over ice and wind-packed snow is very great, often exceeding 1000 km in a single gale (Savile, 1972). Most, if not all, evolution of these four very modern sections surely occurred in the Pleistocene, stimulated by periodic cleavage of populations.

Two other varieties of *Puccinia pazschkei* occur in cordilleran North America: var. *heterisiae* on *Saxifraga mertensiana* and var. *ferrugineae* on S. *ferruginea*. These two hosts seem, from their capsule shapes, to be more modern than their broad leaves suggest. They have retained (or possibly regained) this leaf shape in response to their generally moist and shaded habitats. The placement of S. *mertensiana* in *Boraphila* subsect. *Punctatae* by Engler & Irmscher (1916) is plainly erroneous; and I tentatively assign it to *Boraphila* subsect. *Stellares* which contains other bulbiferous species including S. *ferruginea*. The rusts of these plants presumably diverged from ancestral var. *tricuspidatae*, whose minor distinctions largely reflect selection for the strongly xeric habitats of its hosts, S. *tricuspidata* and S. *bronchialis* ssp. *austromontana*.

Cain (1944) insisted that the center of origin of *Saxifraga* lies in Europe where

the greatest number of sections is recorded. Not only are the European sections oversplit in comparison with, for example, *Boraphila*, invalidating the statistical data: but the European sections vary from moderately to strongly advanced, the primitive ones occurring round the North Pacific rim. Clearly it is in this region that the family and *Saxifraga* originated, a conclusion in which the rust data and comparative morphology are in harmony.

Finally we may ask, when did Saxifragaceae originate? True grazing mammals seem to have appeared in late Eocene (Simpson, 1953); and we may presume that graminoid vegetation, harboring the first long-cycled heteroecious *Puccinia* species, arose at this time. Short-cycled rusts have originated on aecial hosts of such rusts periodically. Thus it is difficult to believe that Saxifragaceae originated before the Oligocene period.

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ANGIOSPERM PHYLOGENY AND GEOGRAPHY

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Abstract

Despite frequent long-range disjunctions among the angiosperms, geography can often have considerable suggestive value in discovering relationships among families and subfamilies and even higher categories. According to my classification and so far as currently known, 72 of 324 families and 78 of 281 additional subfamilies are restricted to one continental area or its oceanic equivalent for a total of 150 of 605 families and subfamilies. Representatives of a good many more families and subfamilies barely reach a second continent. Two small orders, Balanopales and Leitneriales, and six suborders are similarly restricted. Restricted either to the Old World (166) or the New World (71) are 103 families and 134 additional subfamilies for a total of 237 families and subfamilies. Four orders and two suborders are similarly restricted and one additional suborder largely so. Similarly, 90 families and subfamilies are restricted or largely so to the Southern and 74 to the Northern Hemisphere for a total of 164 of the 605 families and subfamilies.

Since the circumscription of these families and subfamilies has largely been accomplished through study of the comparative anatomy and morphology of the constituent plants, it is rather obvious that there is often a marked correlation between classification and geography. Even the widely disjunct larger groups follow very definite patterns in their disjunctions. Thus, a careful study of plant geography can be most helpful in placing dubious taxa. Doubtful genera "out of place" geographically should be restudied with geography in mind. As one example, *Oftia* as the only genus of the largely Pacific Ocean Myoporaceae in mainland Africa seemed out of position geographically. A recent critical study showed it to belong not to the Myoporaceae but to a tribe of Scrophulariaceae well represented in South Africa. The Old World Pittosporales, as I have redefined the order with three suborders, Daphniphyllineae of southeastern Asia and Malesia, the Pittosporineae largely of Australasia, and the Brunineae of southern Africa and Madagascar, are considered in some detail as a relatively large order of 10 families in which geography offered the major clue to its recognition and circumscription. Other taxonomists have each treated the 10 families in five to seven widely separated orders involving a total of 16 different ordinal names.

Despite frequent long-range disjunctions among the angiosperms at various hierarchial levels, a surprising number of families and subfamilies or even higher taxa are restricted in their geographic ranges to single continents or portions thereof. Based upon my revised classification (Thorne, 1968, 1973*b*, 1974*a*, 1974*b*, 1974*c*) and our current knowledge of plant distribution, 72 of 324 families and 78 of 281 additional subfamilies are restricted to one continental area or its oceanic equivalent for a total of 150, or nearly one-fourth, of the 605 accepted families and subfamilies.

A few of these continentally restricted groups, especially well known to American botanists, are such mono- or digeneric, essentially endemic North American families as the dispecific rosalean Crossosomataceae of the Southwest, Fouquieriaceae with 11 species (Henrickson, 1972) in the Southwest and Mexico, Garryaceae with perhaps 15 species of western and Middle America and the Greater Antilles, monospecific Leitneriaceae of the Southeast, primarily western Limnanthaceae with two genera and 11 species, and monospecific Simmondsiaceae of the Southwest and Mexico. A good many more families and subfamilies, like the Sarraceniaceae (17 species in 3 genera), Lecythidoideae (ca. 290 species in 15

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genera) of the Lecythidaceae, and Echeverioideae (ca. 170 species in 3 genera) of the Crassulaceae, barely reach a second continent in the Americas.

Similarly restricted continentally are 13 South American families, including the Caryocaraceae, Gomortegaceae, Lissocarpaceae, Quiinaceae, and Rhabdodendraceae among others. The Brunelliaceae, Maregraviaceae, and Tropaeolaceae are essentially South American too but do reach tropical Mexico of North America. Eurasia, really eastern Asia except for the truly Eurasian monotypic Butomaceae, hosts 17 endemic families including the Cercidiphyllaceae, Crypteroniaceae, Eucommiaceae, Pentaphylacaceae, Stachyuraceae, and Tetracentraceae. Most of them are monogeneric and have only one or very few species. Australasia, taken in the broadest sense to include New Guinea, eastern Melanesia, and southern Polynesia, possesses 16 endemic families, among which are the Corynocarpaceae, Degeneriaceae, Eupomatiaceae, Gyrostemonaceae, and Trimeniaceae, again families mostly with few species or monotypic. Fifteen families are restricted to Africa (some also in Madagascar), 4 more to Madagascar alone (Didiereaceae, Didymeliaceae, Sarcolaenaceae, and Sphaerosepalaceae), and one to the Seychelles (Medusagynaceae). Some of the African families are discussed below.

Two small orders, the Balanopales of Australasia and Leitneriales of the American Southeast, and six suborders, the Brunineae of Africa, Daphniphyllineae, Eucommineae, and Trochodendrineae of eastern Asia, and Fouquieriineae and Limnanthineae of North America, are restricted to part of one continental area or its oceanic equivalent.

Including the continentally restricted groups, 102 families and 135 additional subfamilies for a total of 237 families and subfamilies, about 40% of the total number, are restricted to the Eastern or the Western Hemisphere, 166 to the Old World and 71 to the New World. Similarly restricted are 4 Old World orders: Casuarinales (ca. 65 species in 2 genera), Pandanales (probably far fewer than the listed 700 species in 3 genera), Pittosporales (10 families, 31 genera, and ca. 350 species), and Tamaricales (ca. 120 species in 4 genera); and one suborder, Nepenthineae (ca. 70 species in one genus, *Nepenthes* L.) of the Theales; and one New World order, the Cyclanthales (ca. 180 species in 11 genera) and one suborder Sarraceniineae (17 species in 3 genera) of the Theales (DeBuhr, 1975). One of the biggest and economically most important families restricted to the Old World is the timber family Dipterocarpaceae with perhaps 600 species in 15 genera (map in Thorne, 1973*a*).

With only two species (*Gaimardia australis* Gaud. of the Centrolepidaceae and *Leptocarpus chilensis* (Gay) Mast. of the Restionaceae) reaching the southern tip of South America in the New World is the otherwise exclusively Old World suborder Flagellariineae (4 families, ca. 40 genera, and ca. 370 species) of the Commelinales. In addition to the Restionaceae (ca. 325 species in 35 genera) and Centrolepidaceae (40 species in 5 genera) of the Flagellariineae just mentioned, two other largely Australasian families that barely reach the same Fuegian area of South America are the Epacridaceae (ca. 400 species in 30 genera with *Lebetanthus myrsinites* (Lam.) Endl. ex Dusén in Fuegia and Patagonia) and Stylidiaceae (ca. 160 species in 6 genera with *Donatia fascicularis* Forst. and

Phyllachne uliginosa Forst. in Fuegia), as well as the huge myrtaceous subfamily Leptospermoideae (surely more than 1000 species in perhaps 42 genera with only *Tepualia stipularis* (Hook. ex Arn.) Griseb. in Chile).

Barely reaching Africa and sometimes a bit beyond are one or two species each of the large American families Bromeliaceae (ca. 1400 species in 60 genera) and Cactaceae (perhaps 1500–2000 species in 50–100 genera), and the smaller families Humiriaceae (49 species in 8 genera), Loasaceae (ca. 200 species in 14 genera), Mayacaceae (4–10 species in 1 genus), Rapateaceae (80 species in 16 genera), and Vochysiaceae (200 species in 6 genera) (Thorne, 1973*a*, 1973*c*). Old World families or subfamilies with only one or a few species in the New World, other than the Australasian groups just reaching the subantarctic tip of South America, are the Cneoraceae (3 species in 1 genus), Myoporaceae (ca. 90 species in 3 genera), Pedaliaceae (50 species in 12 genera), Resedaceae (ca. 70 species in 6 genera), and Cotyledonoideae (ca. 310 species in 4 genera) of the Crassulaceae (Thorne, 1973*a*, 1973*c*).

Similarly, 90 families and subfamilies are restricted or largely so to the Southern and 74 to the Northern Hemisphere for a total of 164 of the 605 families and subfamilies. Well-known examples of essentially Northern Hemisphere groups are the Aceraceae (ca. 200 species in 2 genera), Nyssaceae (11 species in 3 genera), Paeoniaceae (33 species in 1 genus), Pyroloideae (ca. 45 species in 4 genera) and Monotropoideae (12 species in 10 genera) of the Ericaceae (Wallace, 1974, and personal communication). Some of the larger groups of the Southern Hemisphere are the South American Calyceraceae (40 species in 4 genera), Malesherbiaceae (35 species in 1 genus), and Myzodendraceae (11 species in 1 genus), Australasian Dampieroideae (ca. 80 species in 3 genera) of the Goodeniaceae, and South African Penaeaceae (ca. 25 species in 5 genera).

Because the circumscription of these families and subfamilies has largely been accomplished through study of the comparative anatomy and morphology of the constituent plants, it is rather obvious that there is often a marked correlation between classification and geography. Even the widely disjunct larger groups follow very definite patterns in their disjunctions, as for example, the tropical American-West African, eastern North American-eastern Asian, Australasian-Fuegian, Mediterranean-American, Californian-Chilean, and similar well-known disjunctions (Thorne, 1973*a*). Thus, a careful study of plant geography can be most helpful in placing dubious taxa. Doubtful genera "out of place" geographically should be restudied with geography in mind.

A couple of recent examples may be instructive. *Oftia* Adans., as the only genus of the largely Pacific Ocean Myoporaceae in mainland southern Africa and Madagascar, seemed out of position geographically. A recent critical study by Dahlgren & Rao (1971) indicates that it belongs not to the Myoporaceae but near *Teedia* Rudolphi of the Scrophulariaceae, with 4 species endemic to South Africa. *Miconia africana* Jacques-Felix, the only African species listed from an otherwise huge American genus (perhaps 1000 species), definitely seemed out of order in Africa, where otherwise the Melastomataceae are linked to Asia rather than to tropical America in their relationships (Wurdack, personal communication).

Examination of the type by Wurdack (1970) proved that *Miconia africana* is not a *Miconia* and not an African collection. It is a Brasilian *Leandra* apparently collected in Brasil. The mistake resulted presumably from a mix-up in labels.

The Old World Pittosporales, as I have redefined the order (Thorne, 1968) with three suborders, the Daphniphyllineae of southeastern Asia and Malesia, Pittosporineae largely of Australasia, and Brunineae of southern Africa and Madagascar, is a relatively diverse and large order of 10 families in which geography offered the major clue to its recognition and circumscription.

As I developed my phylogenetic system of classification over the years by reconstructing what I regard as natural orders, I had a large number of taxa *incertae sedis* that I had ejected from many different widely accepted orders where they surely did not belong. A group of such families and genera from the Old World caught my eye because of their similar geographic distribution and their moderately primitive xylem anatomy. This group of 10 families is treated in five to seven widely unrelated orders in each of four current systems of classification (Melchior, 1964; Cronquist, 1968; Takhtajan, 1969; Hutchinson, 1973) involving 16 different ordinal names. Closest to my treatment is that of Hutchinson (1973), with only five different orders involved and seven families placed in the rather closely related Hamamelidales and Pittosporales. In drawing up a chart of their characteristics, I was struck by the large number of basic characters that they possess in common. Among other features, they combine generally simple, exstipulate leaves; unspecialized xylem; actinomorphic flowers with a definite number of stamens opposite the sepals; syncarpous pistil; often subapical, pendulous, anatropus ovules; seeds with a minute embryo in abundant endosperm; and variable habit, though most are small trees, shrubs, or twining undershrubs of relatively mesic habitats. There are also strong tendencies in the order toward apetalous or naked flowers, dioecism, epigyny, crowding of the small flowers into bracteate spikes or heads, porous anther dehiscence, and parietal placentation in monolocular ovaries.

Daphniphyllum Blume (9 species), ejected from the Euphorbiaceae and the sole genus of the Daphniphyllaceae and Daphniphyllineae, retains the most primitive foliage and xylem in the order but is specialized in its unisexual, apetalous flowers with imperfectly 2-locular ovary and 1-seeded drupes. The small shrubs to large trees have alternate, entire, coriaceous, pinnately-nerved leaves; xylem with small, solitary, angular, very long vessel elements with scalariform perforation plates and scalariform to opposite intervascular pitting; diffuse parenchyma; markedly heterocellular rays with numerous uniseriates; and long tracheids or fiber-tracheids with distinctly bordered pits. The nine species, 1–20 meters tall, are plants of moist warm-temperate to tropical forests of southeastern Asia, from Japan and western China to New Guinea and Ceylon (Huang, 1965).

The Pittosporineae retain the least specialized flowers but have the most specialized xylem in the order. The largely Australasian Pittosporaceae (ca. 200 species in 9 genera), the largest family, have typically bisexual, actinomorphic, pentamerous flowers with biseriate perianth of mostly distinct, imbricate parts, and ovary superior with 2–5 complete or incomplete locules and numerous ovules

on axile or parietal placentae. The xylem has vessels with simple perforation plates and alternate, small intervascular pitting; sparse, paratracheal parenchyma; almost homocellular rays with few uniseriates, and moderately-short, septate libriform fibers with simple or vestigially bordered pits. *Pittosporum* Banks ex Soland., the largest genus with about 160 species, has a range (map in Thorne, 1973*c*) that exceeds the combined ranges of all other genera of the whole order. The three genera of the Tremandraceae, with perhaps 25 species, are endemic to Australia, especially southwestern Australia, and have usually been placed near the Malpighiaceae, presumably because of the appendaged seeds and porous anther dehiscence. However, some of the more specialized Australian Pittosporaceae and the two Australian species of *Byblis* Salisb. (one of which is also in New Guinea), the sole genus of Byblidaceae, have porous anther dehiscence, as does *Roridula* Burm. f. of South Africa, the sole genus of the Roridulaceae in the Brunineae. In addition, there is great similarity in floral morphology, pollen and xylem, as well as in the general facies of the plants, flowers, and fruits.

The Brunineae are exclusively African and Madagascan, and consist of simple-leaved shrubs or undershrubs of moist habitats in otherwise xeric areas or tuberous-stemmed, pinnatisect-leaved herbs (*Hydrostachys* Thous.) specialized for existence in seasonal streams. *Geissoloma* Lindl. ex Kunth (1 species), *Grubbia* Endl. (3 species), *Hydrostachys* (ca. 30 names listed), *Myrothamnus* Welw. (2 species), and *Roridula* (2 species), each representing a distinct family, and the more varied Bruniaceae (ca. 75 species in 12 genera) have similar very primitive xylem with small, solitary vessels with many-barred scalariform perforation plates; chiefly diffuse parenchyma; narrow, heterocellular rays; and tracheids or fiber tracheids generally with prominent borders. The often apetalous flowers are mostly aggregated in dense spikes or heads; the pollen grains are mostly tricolporate and subspheroidal; the fruit is usually a capsule; and the plants, except for *Hydrostachys*, are mostly small shrubs with small, evergreen, simple leaves. The African and Madagascan genera *Myrothamnus* and *Hydrostachys*, though adapted to unlike habitats, share a surprising number of characteristics: leaves with dilated bases; naked, imperfect flowers, sessile and solitary in the axil of each bract of a tight spike; dioecism; syncarpous ovary with divergent styles; similar pollen grains united in tetrahedral tetrads; and fruit a small capsule with numerous seeds.

To test the validity of my classification of the Pittosporales, I have assembled for study representative specimens of all the genera. I have considerable personal field acquaintance with the families of the Pittosporineae in Australia, New Guinea, New Caledonia, and other parts of the Pacific but only arboretum or herbarium experience with the families of the other two suborders. An attempt some years back to obtain grant funds to support a trip to South Africa to study the Brunineae was unsuccessful. However, I have encouraged several students and colleagues to study representative taxa of the order. Studies were undertaken by T. C. Huang (1965) on *Daphniphyllum*, Mark Parratt on the Tremandraceae, and more recently by Sherwin Carlquist on the whole group. Prof. Carlquist has very recently returned from an extensive collecting trip to

Western Australia to gather all possible material of the Pittosporineae, just as earlier he scoured Malaysia for *Daphniphyllum* and *Pittosporum*, and South Africa for Brunineae and *Pittosporum*. We await with the greatest interest his findings on the anatomy of these plants. I am grateful to him for suggestions and field information about the members of the Pittosporales in this paper.

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MODERN PROBLEMS OF THE YEARS 1492–1800 IN THE LESSER ANTILLES

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In 1937, H. E. Box, collecting in Antigua, gathered a sterile specimen and a few fruits from the ground beneath an unrecognized tree. Fourteen years later he concluded the material represented a new species, for which he published, with W. R. Philipson, the name *Mastichodendron sloaneanum*. The holotype, however, was a collection made in 1687 by Sir Hans Sloane in Barbados (Box & Philipson, 1951). The species has not been collected again in Barbados since Sloane's visit, nor in Antigua since Box made his collection. Although it is unusual for a plant to be described 264 years after being collected, Box and Philipson were able to trace accounts which may refer to this plant through the literature of the eighteenth century. However, this type of search may not always be a profitable enterprise.

1492–1699

The first botanical observations of the Lesser Antilles, in the accounts of the four voyages of Christopher Columbus, have been the subject of speculation in publications by Samuel Eliot Morison. Aided by the Cuban botanists, H. León, H. Alain and J. C. Carabia, Morison (1942, 1955, 1964) has reported descriptions applicable to such useful or edible plants as the calabash, agave, aloe, royal palm, pineapple and tobacco. The *History of the Indies*, written by J. Fernandez de Oviedo in 1535, also records botanical observations for Hispaniola, Panama and Colombia.

Since the seventeenth century, there have been general accounts of exploration which have an application to current botanical nomenclature. John Smith's *Travels and Observations* (1630) relates to the island of St. Kitts, and his description of "Masticke" has been associated by Box & Philipson (1951) with the widespread *Mastichodendron foetidissimum.*

The work of Jan de Laët (*Novus Orbis seu Descriptionis Indiae Occidentalis*, Libre XVIII), published in 1633, is referred to by Linnaeus in *Species Plantarum* (1: 192. 1753). The "cainito" of de Laët may be the source of the specific epithet chosen for *Chrysophyllum cainito*, although the area of origin is not designated. This is the earliest report from the Lesser Antilles used by Linnaeus, but several subsequent publications of historic value he did not consult. J. B. du Tetre (*Histoire Général Antilles Habituées par les Français*) visited St. Kitts, Guadeloupe, Martinique, St. Martin, St. Barts, Les Saintes, St. Lucia and Grenada between 1650 and 1656. In 1657 Richard Ligon published *A True and Exact History of the Island of Barbados*. De Rochefort traveled from Tobago to St. Croix and wrote of the medicinal and useful plants in his *Histoire Naturelle et Morale des Îles Antilles*, published in 1658.

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The visit of Sir Hans Sloane to the Caribbean area from 1687–1689 truly marked the beginning of botanical knowledge of the islands. As a medical doctor to the governor of Jamaica, where he spent most of his time, Sloane gathered specimens which are preserved in the British Museum (Natural History). He reported his observations in two publications, *Catalogus Plantarum Quae in Insula Jamaica Sponte Proveniunt*, of 1696, and *A Voyage to the Islands of Madera, Barbados, Nieves, S. Christophers and Jamaica*, 1707–1725. Linnaeus's references to these works are many. Sloane apparently encouraged or engaged others to collect natural history specimens for him, for credit for collections is given to Claudius Hamilton, James Reed, and Captain Thomas Walduck for material from Barbados, and to J. Dickenson for plants from Bermuda. *Hortus Kewensis* (1789), attributed to William Aiton, lists many taxa from the West Indies, supposedly introduced to cultivation in Europe in the period of 1714–1733, which may be a residual benefit of Sloane's voyage.

In 1689, two French botanists collected in the Caribbean area. Charles Plumier, as a missionary priest, and J. D. Surian, as botanist for the king, worked together on Martinique and Haiti; and separately, Surian in the Guianas and Plumier briefly in St. Kitts, Guadeloupe and St. Vincent. Specimens were collected and are preserved today in the herbaria at Paris, but the full story and importance of these remain to be worked out. Stafleu (1967: 360, 461) presents the generally accepted view of this material. For Plumier, Stafleu reported, "The types of Plumier's American plants are his original drawings. Further elucidation is provided by Surian's herbarium; in several cases the Surian plants may be the actual types of Plumier species." For Surian, Stafleu stated, "Surian accompanied Plumier to the West Indies in 1689–1690. During the trip Plumier made the drawings and the descriptions, whereas Surian made the collections. The extensive herbarium in book form came to the hands of the Jussieu family and is now at P. It contains a great many plants that are referable to Plumier species and is for that reason an important, although hitherto hardly used, source of information." Plumier's excellent drawings were used by Burman for the preparation of the *Plantarum Americanarum Fasciculus*, now regarded as a very poor rendition of the originals. The descriptions likewise suffered in the reproduction. Dr. Alicia Lourteig is now undertaking a transcription of the original manuscripts. If this can be published with reproduction of the original illustrations, Plumier's valuable work can be made available. It has also been possible to associate specimens attributed to Surian with the drawings and descriptions of Plumier.

Between 1691 and 1696, Leonard Plukenet published engravings of plants sent to him from Barbados in his *Phytographia*. These references are cited by Linnaeus. At the close of the seventeenth century and beginning of the eighteenth (1694–1705), Jean Baptiste Labat visited Grenada, Becquia, Barbados, St. Vincent, St. Lucia, Martinique, Les Saintes, Dominica, Guadeloupe, St. Barts, St. Kitts, Saba, St. Martin and the Virgin Islands en route to Hispaniola. His *Nouveau Voyage aux Iles de l'Amerique*, published in 1724, refers to plants of the area. No specimens are known, but Linnaeus may have drawn *Chrysophyllum icaco* from the Labat reference to *Prunus icaco* (Sp. Pl. 513. 1753.).

1700–1753

This half-century saw the introduction of plants and seeds to the gardens of Europe, and was marked by the botanical collections of Mark Catesby, William Houstoun and Patrick Browne. Britton & Millspaugh (1920) noted that "Thomas Walker, Chief Justice for the Bahama Plantation, sent plants from New Providence to James Petiver in London" at the request of Mr. Robert Ellis. Mark Catesby in 1725 visited the Bahamas and, although he made few collections, he did ship propagating material to European gardens in addition to executing drawings and descriptions. Francis Dale (1730–1733) also sent plants and seeds to be raised in England, along with some dried specimens. William Houstoun collected plants in Jamaica, Cuba, and the state of Veracruz in Mexico for Philip Miller between 1729 and 1733. Houstoun's notes on these collections exist in manuscript form in the Linnaean Society Library, and were frequently cited as polynomials by Linnaeus in *Species Plantarum*. These notes are much needed today in published form. They might be used, for example, to aid in the identification of Houstoun specimens recently discovered in the Petre collection at the Sutro Library in San Francisco (Ewan, 1970). Several of Houstoun's collections were subsequently published as new species, with the epithet "barbadensis," suggesting that Houstoun visited other islands of the Antilles. However, in all cases examined, the species are known only from Mexico, and the implication of Barbados is erroneous. Linnaeus did cite a variety of *Dorstenia contrajerva* based on a reference to a paper by Houstoun, with a distribution indicated as "nova Hispania, Mexico, Peru, Vera Cruce, insula Vicentii." No verification of this reference to St. Vincent can be found.

In 1746 Patrick Browne visited Barbados, Montserrat, Antigua and St. Kitts, although his principal botanical contribution was on Jamaica. Linnaeus acquired Browne's Jamaica herbarium through Collinson in 1758, two years after the publication of Browne's *Civil and Natural History of Jamaica*. Browne's possible collections from the Lesser Antilles have not been identified as such.

In 1750 Rev. Griffith Hughes published *The Natural History of Barbados*. Although the plant illustrations by G. D. Ehret are excellent, the descriptions are "fragmentary and inaccurate" (Gooding *et al.*, 1965: ix), and no herbarium specimens are known.

1753–1800

The publication of *Species Plantarum* in 1753 marked the beginning of modern botanical nomenclature through the use of binomial names for species, and the end of the acceptance of the polynomial description. However, the coverage of the flora of the Antilles in the *Species Plantarum* was not extensive, and Grisebach (1864: vii), in the preface to his *Flora of the British West Indian Islands*, noted that "Baron Jacquin, the Austrian, and Ol. Swartz, the Swedish botanist, are the fundamental authors on the vegetable productions of the British West Indies." To this statement should be appended a reference to the publications of Martin Vahl for the Danish islands in the Leeward group of the Lesser Antilles.

Nicolaus Joseph Jacquin collected in the Caribbean area from 1755 until 1759

as a representative of the Emperor of Austria, gathering plants for the gardens and greenhouses of Schoenbrunn. Living specimens were collected, drawings and descriptions were completed in the field, and some dried specimens were prepared. It had generally been assumed that the herbarium specimens were lost or destroyed, but these specimens are now frequently discovered in the herbaria of Europe. A systematic search for the Jacquin specimens would be profitable at this time, using the original name as well as its modern equivalent as a guide. Upon his return to Europe Jacquin published, perhaps hastily, a listing of his discoveries as *Enumeratio Systematica Plantarum* in 1760. These names, validly published with very brief descriptions, were elaborated upon and often illustrated in the *Selectarum Stirpium Americanarum Historia*, issued in 1763 (Howard, 1973*a*). Additional descriptions were supplied, often with changes or cross references, in *Observationum Botanicarum*, 1764–1771, and in *Plantarum Rariorum Horti Casearei Schoenbrunnensis*, 1797–1804. Each volume is related to the others, but a careful cross reference study has been lacking and is needed. It appears evident that many of Jacquin's plants, readily identifiable, have not been considered in modern taxonomic work. Jacquin cites collections made in Cuba, Jamaica, Hispaniola, St. Martin, St. Eustatius, Martinique, Grenada, Curaçao, Venezuela and Colombia. Grisebach indicated that Jacquin also visited St. Kitts and St. Vincent.

In 1758 the Royal Society, London, offered rewards for the improvement of agriculture and horticulture in the American colonies. The first prize offered was "a gold medal for the first person bringing mango seeds to England to be sent to the West Indies for planting" (Howard, 1954). In 1760 the list for prizes included olives, opium, cinnamon, nutmeg, mace, sarsaparilla, aloe, safflower, indigo, cotton, annatto, vanilla, cloves, pepper, camphor, quinine, various tinctorial plants and ornamental woods. Many of the colonists tried individually to import the plants, not only for the prizes, but for the potential market of profitable crops. In 1765 the governor of the newly acquired Windward islands supported a local project of creating a botanical garden for the purpose on the island of St. Vincent. Thus, the first botanical garden in the West Indies was established on one of the smaller islands. Dr. George Young, a local medical officer and an ardent horticulturist, was appointed the first director. Between 1765 and 1783 he developed the garden into a place of beauty and scientific importance by introducing plants from many areas. The dried specimens of plants of St. Vincent and of his introductions from other areas are still preserved today at Kew. Planters on Jamaica, envious of the usefulness of the St. Vincent botanical garden, petitioned their government for a botanical garden, and the one at Bath was begun in 1779, to be followed by others.

The history of the botanical gardens in the French islands has not been worked out, but the episode of La Sainte Anne suggests they did exist. In February of 1782, Jean-Nicolas de Cere, then in charge of the Jardin du Roi on the Île de France (Mauritius), wrote to the governor general of St. Dominique (Hispaniola), stating he was sending him some plants in a ship to sail the following day. A list of the plants included mangoes, screw pine, jackfruit, cinnamon, carambola, bilimbi and

others. The ship, La Sainte Anne, was captured by Captain Marshall of Lord Rodney's fleet in June, 1782. Marshall's ship was appropriately named "Flora." The prize of plants was taken to the recently established garden at Bath, and included a mango numbered 11 in the inventory. The mango is known today in Jamaica by that designation, no. 11. A species of *Moringa* was also included, and this may well be the original introduction of *Moringa oleifera* into the West Indies. There is also the suggestion that plants of nutmeg, clove and black pepper were aboard but were destroyed before the capture. These three crops were prized by the French, and their export at that time was forbidden. The destination of the plants in Hispaniola is still unknown. Presumably there might have been a botanical garden to receive them, but if so, no records of its location or existence are found in the literature. By 1803 there were records indicating an interchange of plants between a botanic garden in Haiti (its curator being F. Richard de Tussac) and James Wiles of the Bath botanic garden (Powell, The Botanic Garden, Liguanea, Institute of Jamaica, 1972.).

The success of the botanical gardens apparently attracted collectors to the Antilles. In 1767 Jean Baptiste LeBlond, a Frenchman, visited Martinique and St. Lucia in addition to northern South America. Sometime before 1773, Christen F. Rottbøll, a Dane, collected Cyperaceae and Gramineae in the area. Francis Masson, a Briton, known for his work in Africa, collected on Barbados, Grenada, St. Lucia, Antigua, St. Kitts, Nevis and St. Eustatius en route to Jamaica in the period of 1779–1780.

It is not known how or exactly when Olof Swartz, the Swedish botanist, began his interest in the vegetation of the Caribbean Islands. He visited Jamaica, Cuba and Hispaniola from 1784–1786, and in 1788 published his *Nova Genera et Species Plantarum seu Prodromus*. This scanty volume, reporting many new genera and species through very brief descriptions, was followed by *Observationes Botanicae* in 1791, *Icones Plantarum Incognitarum*, 1794–1800. and the massive *Flore Indiae Occidentalis*, 1797–1804, each of which elaborated on the descriptions previously published and added new ones. As with the publications of Jacquin, the Swartz publications are interrelated and require cross-referencing for name changes and for typifications. Swartz consulted the collections in several European herbaria and referred specifically to collections of other botanists. Swartz was so generous with his own material that the problem of typification of his species will require the search of many modern herbaria. The collectors of West Indian plants to whom he refers include Scandinavian, English and French botanists.

In 1785 Alexander Anderson replaced George Young as superintendent of the botanical garden on St. Vincent. It was during his administration that the Bligh expeditions to the Pacific returned the breadfruit and 508 other plants to the West Indies (Powell, The voyage of the plant nursery, H.M.S. Providence, 1791–1793. Institute of Jamaica. 1973.). Anderson, too, collected widely. His collections from St. Vincent, Martinique, St. Lucia, Barbados, Grenada and South America were cultivated at the botanical garden and sent to Europe as exsiccatae. Unfortunately, the designation "St. Vincent," commonly associated with his collections, should be

questioned in determining the specimens or in declaring geographic distribution. Anderson served as director from 1785 until his death in 1811.

Until the close of the eighteenth century the collectors working in the Antilles were so numerous that they must have encountered each other. Samuel Fahlberg collected on St. Barts, Guadeloupe, Martinique and St. Kitts in 1785. Paul Erdman Isert collected on St. Eustatius, Guadeloupe, Martinique and in the Virgin Islands in 1785–1786. J. Gregg (spelled with one or two g's) collected on Dominica and Barbados in 1786. Also in 1786–1787 du Ponthieu was on Barbuda, Antigua, Montserrat, Guadeloupe, Dominica, Grenada and Tobago; Louis C. Richard on Antigua, Anguilla, Guadeloupe, Martinique, Barbados, as well as the Virgin Islands, Puerto Rico and Hispaniola; and F. Richard Tussac on Martinique and Haiti. In 1788 Bengt Anders Euphrasen collected on St. Barts, St. Eustatius and St. Kitts. The majority of these collectors are cited in the publications of Swartz.

Martin Vahl, a student of Linnaeus and later a professor at Copenhagen, published three works between 1790 and 1807 which describe plants of the Antilles. His *Symbolae Botanicae* (1790–1794), *Eclogae Americanae* (1796–1807), and his *Icones Illustrationi Plantarum Americanarum* (1798–1799) are largely based on the collections of von Rohr, Ryan, Martfelt, West and Ledru. Martfelt made collections on Guadeloupe and Barbados in 1791. Julius von Rohr in 1786 collected on Martinique, Guadeloupe, Barbados, Antigua, Anguilla, the Virgin Islands, Puerto Rico and Hispaniola. Hans West collected with André Pierre Ledru on Martinique in 1797, but many of West's specimens are without localities, while most of Ledru's are from Puerto Rico and the Virgin Islands. Dr. John Ryan, according to Stearn (1965: 270), was an English medical man and a plantation owner on Montserrat. He was known to be a friend of von Rohr; hence, his undated collections may be of the same period. He returned to England in 1792, but because of customs difficulties sent his plants to Copenhagen, where Vahl described many, eventually sending the collection to Banks in England.

The century ended during the active period of Felix Louis L'Herminier (1798–1815), a pharmacist on Guadeloupe, who also made large collections on Antigua, St. Barts, St. Eustatius and Saba, and in the Virgin Islands.

The abundance of collectors, and the frequency of the derived publications, can be seen in the following listing. Since many of the publications were issued in parts, the difficulty in correlating the parts and establishing priority of publication is evident. To this list of significant volumes concerning the Antillean flora should be added Aublet's *Histoire des Plantes de la Guiane Française*, published in 1775. Aublet collected in French Guiana between 1762 and 1764, and many of the plants he described have ranges extending into the Lesser Antilles. L'Heritier's *Sertum Anglicum* (1787) is an example of the horticultural literature of Europe which occasionally has competing descriptions of Antillean plants.

Linnaeus, *Species Plantarum*. 1753.
Loefling, *Iter Hispanicum*. 1758.
Linnaeus, *Systema Naturae*. ed. 10. 1759.
Jacquin, *Enumeratio*. 1760.
Linnaeus, *Species Plantarum*. ed. 2. 1762, 1763.

Jacquin, *Selectarum*. 1763.
Jacquin, *Observationum Botanicarum*. 1764–1771.
Linnaeus, *Mantissa Plantarum*. 1767–1771.
Aublet, *Histoire des Plantes*. 1775.
Linnaeus, filius, *Supplementum Plantarum*. 1781.
Jacquin, *Collectanea*. 1786–1796.
Swartz, *Prodromus*. 1788.
L'Heritier, *Sertum Anglicum*. 1789–1792.
Swartz, *Observationes Botanicae*. 1791.
Swartz, *Icones Plantarum*. 1794–1800.
Vahl, *Eclogae Americanae*. 1796–1807.
Swartz, *Flore Indiae Occidentalis*. 1797–1804.
Jacquin, *Plantarum Horti Schoenbrunnensis*. 1797–1804.
Vahl, *Icones Plantarum Americanarum*. 1798–1799.

Modern Period

The publication of competitive studies so close together resulted in the same species being described as new by different authors. Subsequent publications concerning the plants within the Antilles also have been nationally oriented. There are floras of Barbados (Maycock, 1830), Cuba (León 1946; León & Alain, 1951, 1953, 1957; Alain, 1962), Hispaniola (Moscoso, 1943), Jamaica (Fawcett & Rendle, 1910–1936), Puerto Rico (Britton & Wilson, 1923–1930), as well as the Dutch Islands (Boldingh, 1913), the British Islands (Grisebach, 1864) and the French Islands (Duss, 1897), which consider primarily the plants from the circumscribed area. More modern floras, such as *Flora of Barbados* by Gooding *et al.* (1965), *Flowering Plants of Jamaica* by Adams (1972), and *Flora of Trinidad and Tobago* by Williams, Cheesman & Collaborators (1928–1955) are more comprehensive in their consideration of extraterritorial taxa. However, in general the authors of floras of Central American countries, or those of northern South America, rarely consider the plants of the Antilles, and vice versa.

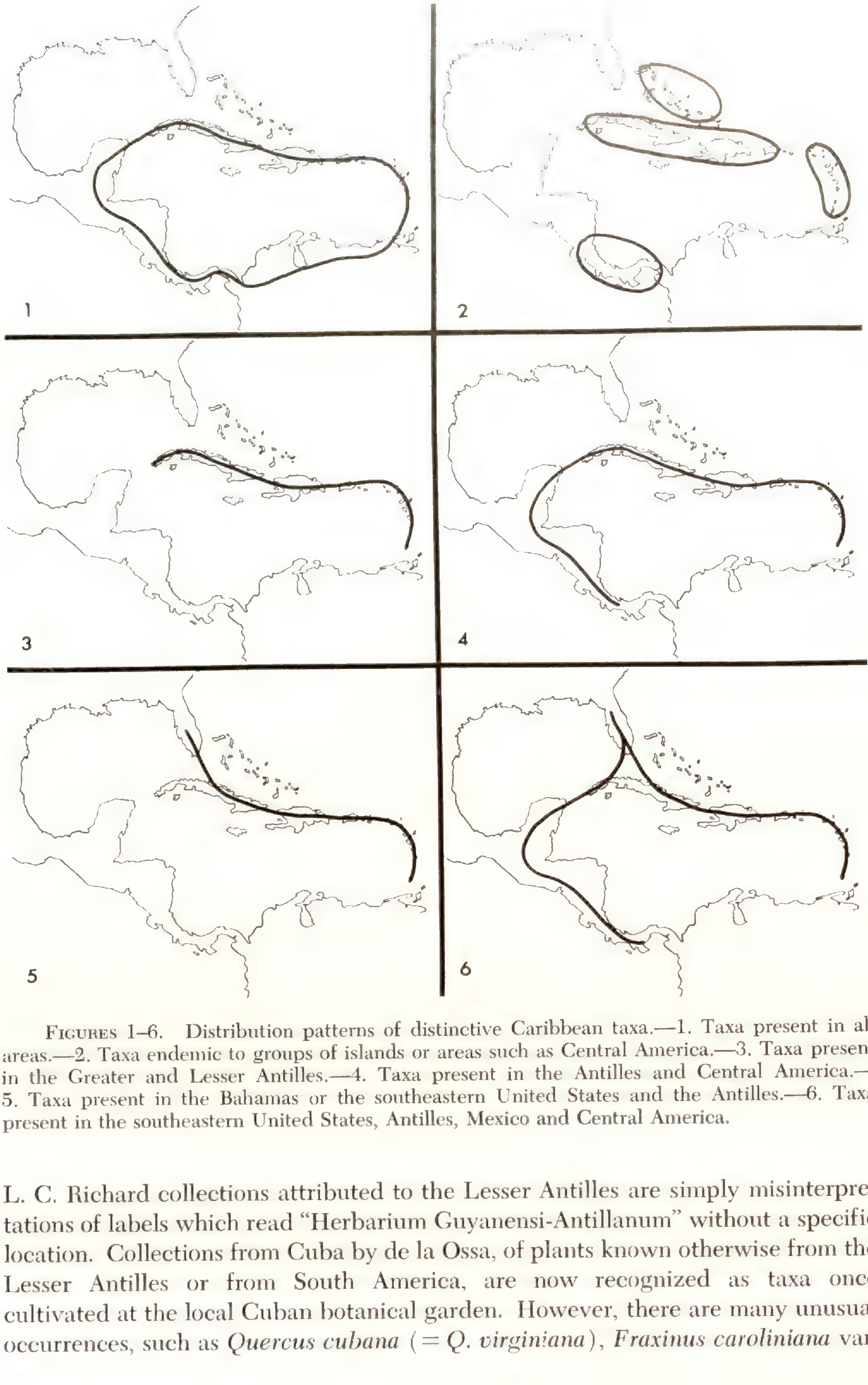
Monographs of genera of wide distribution are few, and it is probable, if not evident, that the plants of the Caribbean periphery are still overdescribed. It is often difficult to determine whether a given species is truly native to the area under consideration, or is the result of a deliberate or accidental introduction. Pre-Columbian introductions, primarily of food or fiber plants, are known as well as are those of more recent times by the explorers for botanical gardens. The breadfruit (*Artocarpus altilis*), the ackee (*Blighia sapida*), the Brazilian rubber (*Hevea brasiliensis*), the India rubber vine (*Cryptostegia grandiflora*) and the coralita (*Antigonon leptopus*) can all be documented as deliberate introductions of useful or ornamental plants. The French cotton (*Calotropis procera*), the rose apple (*Syzygium jambos*) and the quick stick (*Gliricidia sepium*) are undocumented introductions, as are many of the common weeds. By careful elimination it is possible to select a "native" flora which can be considered in relation to the known distribution of related taxa.

The Antilles has had one so-called endemic family, Picrodendraceae, with

a single genus and four species. Recent careful study has shown this to be monotypic and more accurately assigned to the Euphorbiaceae. Within the Caribbean area, certain families, genera or species of distinctive morphology—*e.g.*, Dichapetalaceae, Cunoniaceae, Proteaceae: *Spathelia*, *Tibouchina*, *Wullschlaegelia*; *Baccharis cotinifolia*, *Bontia daphnoides*, *Comocladia ilicifolia*, *Voyria* (*Leiphaimos*) *parasitica*—allow firm conclusions to be drawn on ranges and relationships. A basic number of eleven patterns of distribution can be drawn within the Caribbean periphery, ranging from pan-Caribbean to single area endemics. Examples of these patterns at the generic level have been given by Howard (1973*b*).

1. Taxa as species, genera or families which are present in all areas and occur as seacoast or strand plants to those of higher elevations (Fig. 1).
2. Endemics to groups of islands or areas such as Central America, the Greater Antilles or the Lesser Antilles (Fig. 2).
3. Endemics to single areas or islands. The various soils of the Antilles appear to have characteristic development of endemic species. Noteworthy are the endemics of serpentine soils in central Cuba; the bauxite plants of Hispaniola; or those occurring on outcrops of gypsum rock. Recent authors have estimated the percentage of specific endemism to be 50% in Cuba (Alain), 33% in Hispaniola (Moscoso), 20% in Jamaica (Adams), 4% in Puerto Rico (Britton and Wilson), 13% in the Bahamas (Britton and Millspaugh), and 12% in the Lesser Antilles (Howard)—not illustrated.
4. A range of the Greater Antilles–Lesser Antilles with the taxon lacking in Central America or South America (Fig. 3).
5. An occurrence in Central America, the Greater Antilles, into the Lesser Antilles but not found in South America (Fig. 4).
6. A range including either the Bahamas or southeastern United States into the Greater Antilles and the Lesser Antilles, but absent from Central America and South America (Fig. 5).
7. A range from the southeastern United States into the Greater Antilles and the Lesser Antilles, as well as into Mexico and Central America, but absent from South America (Fig. 6).
8. Taxa primarily of northern South America with range extensions northward into the Lesser Antilles (Fig. 7).
9. A range from Central America, across northern South America and northward in to the Lesser Antilles, but missing from the Greater Antilles (Fig. 8).
10. A pattern of distribution showing an occurrence in the Greater Antilles, the Lesser Antilles and northern South America, but not in Central America (Fig. 9).
11. A center of distribution in Central America with range extensions into the Greater Antilles and northern South America, but not occurring in the Lesser Antilles (Fig. 10).

The occurrence of single species with long-range disjunct distributions generally fits into these distribution patterns. However, many are suspect. Many of the



FIGURES 1–6. Distribution patterns of distinctive Caribbean taxa.—1. Taxa present in all areas.—2. Taxa endemic to groups of islands or areas such as Central America.—3. Taxa present in the Greater and Lesser Antilles.—4. Taxa present in the Antilles and Central America.—5. Taxa present in the Bahamas or the southeastern United States and the Antilles.—6. Taxa present in the southeastern United States, Antilles, Mexico and Central America.

L. C. Richard collections attributed to the Lesser Antilles are simply misinterpretations of labels which read "Herbarium Guyanensi-Antillanum" without a specific location. Collections from Cuba by de la Ossa, of plants known otherwise from the Lesser Antilles or from South America, are now recognized as taxa once cultivated at the local Cuban botanical garden. However, there are many unusual occurrences, such as *Quercus cubana* (= *Q. virginiana*), *Fraxinus caroliniana* var.

FIGURES 7–10. Distribution patterns of distinctive Caribbean taxa.—7. Taxa primarily of northern South America extending into the Lesser Antilles.—8. Taxa present in Central America, northern South America and the Lesser Antilles.—9. Taxa present in the Antilles and northern South America.—10. Taxa centered in Central America and extending to the Greater Antilles and northern South America.

cubensis, *Juglans insularis*, *Dracena cubensis*, and *Vallisneria americana* and *V. neotropicalis* which are to be regarded as long-range extensions.

Recently family treatments for the Lesser Antilles have been prepared for the Orchidaceae by Garay and Sweet, the Myrtaceae by McVaugh, and the Piperaceae by Howard. These studies have permitted a re-evaluation of the taxa previously recognized from the area.

The completed study of the Orchidaceae recognized 44 genera, of which 21 were monotypic, but none was endemic to the area. One hundred forty-one species were recognized, with 68 synonyms assigned to these species, excluding the basionym and varieties. Some species were obviously cultivated, *e.g. Vanilla planifolia*; or probably escaped from cultivation, *e.g. Epidendrum cochleatum*. All of the distribution patterns given above were represented except no. 11. Some questions persist, however, for two taxa, *Cyrtopodium andersonii* and *Chloraea*, represent "endemic species" of St. Vincent. Both were collected only once, and are represented by single specimens prepared by the director or an associate of the botanic garden in St. Vincent. Both genera are South American, with no other representatives in the Antilles. Both taxa suggest plants not yet collected in South

America, and not necessarily endemic species of St. Vincent. Sixteen species are considered endemic to the Lesser Antilles, representing 11%.

The Myrtaceae comprised 15 genera, of which 8 were monotypic; but again, none endemic to the Lesser Antilles. Sixty-two species were recognized, with 93 synonyms for those species; again excluding the basionym and additional varieties. In this treatment several species from Central America or northern South America were recognized for the first time as synonyms of older species from the Lesser Antilles. Species of *Psidium* and *Syzygium* were recognized as cultivated or escaped and now weedy species. Ten species are considered endemic to the Lesser Antilles, *i.e.*, 15%.

The Piperaceae comprised four genera, of which two were monotypic, but neither was endemic to the area. Twenty-nine species were recognized, with 103 specific and 52 varietal synonyms. The large number of species which were placed in synonymy were described by Trelease and Stehlé, together or separately, for these men considered many plants to be endemic to Martinique or Guadeloupe, ignoring frequently the identical material from the intervening island, Dominica. This study did not take serious consideration of taxa described from Central America and northern South America, due to the overwhelming numbers of taxa in such related areas. A recent study by Berger (1971) of the Piperaceae of Costa Rica, for example, recognized 164 species from that single country, with an additional 128 names listed in synonymy. Six species of Piperaceae were recognized as being cultivated at one time in the old botanical garden at St. Pierre. One taxon is currently cultivated, *Piper nigrum*. One species, *Peperomia pellucida*, has become weedy. There are but four species recognized as endemic to the Lesser Antilles, representing less than 3% of the total species reported.

Throughout this study of the flora of a relatively few small islands, the nature of its problems became evident. There are old collections supportive of the species described by Linnaeus, Jacquin, Aublet, Swartz and Vahl, but the majority of these species have not been typified. The dates of publication of the several major works of the area overlap, presenting bibliographic problems.

Few monographers have considered at one time all of the species of a genus for the pan-Caribbean area, permitting an excessive number of endemics to be reported. The area and its plant life, however, offer a real challenge to the taxonomist with a broad perspective.

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SUMMARY OF THE BIOGEOGRAPHY SYMPOSIUM

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The preceding eight papers provide a broad sampling of current thought in biogeography, a field which has been revitalized in recent years. Approaching a variety of interesting problems, the authors have contributed several kinds of new insights or conclusions, based on the kind of sound taxonomic analysis that is necessary before any biogeographic conclusions can be drawn. The complexity of such taxonomic analysis for such an area as the Lesser Antilles is well illustrated by Howard (this symposium). Some of the main themes emerging from this symposium were the following: continuity in the Southern Hemisphere; discontinuity between the Northern and Southern Hemispheres; changing routes of migration in the Northern Hemisphere; Tertiary aridity in the southeastern United States; new insights into the disjunction between the Appalachians and the Mexican-Central American Highlands; and the role of biological information in interpreting geological evidence.

SOUTHERN HEMISPHERE CONTINUITY

There have been far greater opportunities for migration in the Southern Hemispere than most biogeographers accepted as recently as a decade ago (*e.g.*, Darlington, 1965). Brundin's (1966) conclusion on biological grounds that first Africa, then New Zealand, then Australia and finally South America separated from Antarctica and membership in a Southern Hemisphere land mass has been confirmed fully on geological evidence. Similar conclusions have been reached by Edmunds and elegantly summarized in this symposium, using evidence from a different group of insects, the mayflies. Another outstanding recent paper in this area is that of Rosen (1974) on salmoniform fishes. The existence of a cool-temperate migration route between South America and Australia which prevailed until at least the Late Eocene now appears to be generally accepted (Raven & Axelrod, 1972).

The likelihood of migration across the present area of the Indian Ocean between West Gondwanaland (South America + Africa) and Australasia in mid-Cretaceous time (~ 110 m.y. BP) by such groups as marsupials (Raven & Axelrod, 1974), has been strengthened by recent geological evidence (*e.g.*, Sclater & Fisher, 1974; Markl, 1974). If the plant order Pittosporales proves to be a natural group, the patterns discussed by Thorne (this symposium) could be explained in a similar fashion, although perhaps more recent and involving sweepstakes dispersal over water. The geographical position of *Daphniphyllum* in Asia, however, suggests greater antiquity if it is indeed directly related to the other families placed by Thorne in this order.

One of the major new patterns emerging in this area is that Madagascar and India may have been joined at a time when Madagascar and Africa were not

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joined, as suggested by Edmunds in this symposium on the basis of new biological evidence. It has recently been suggested that India and Madagascar may not have been joined directly, but rather by a foundered Mascarene landmass (Kutina, 1975). The absence of primary freshwater fishes in Madagascar coupled with the presence of dinosaurs in the Cretaceous remains an enigma, and the geological evidence does not unequivocally support a particular separation sequence of absolute timing for this biologically fascinating island. In contrast with the assumptions of most geologists, Kutina (1975) suggests that Madagascar may occupy essentially its original position and never have been joined to Africa at all, a configuration that might help to explain some biological relationships—the dinosaurs might have come to Madagascar from the north or via Asia or even India.

Discontinuity between Northern and Southern Hemispheres

In addition to the Tethys Sea, which divided Eurasia from Africa and Australia from the Jurassic onward, the considerable expanse of ocean which existed between North and South America in Cretaceous and Paleogene time, discussed in detail by Raven & Axelrod (1974), now appears to have been an important biogeographic feature. Separation between Northern and Southern Hemispheres at these times appears to have been almost total, with the possible direct links apparently only those seemingly temporary ones which existed between Europe and Africa approximately 80–63 m.y. BP (Cooke, 1972; Dewey *et al.*, 1973). Following a period of even wider separation, possibly with a brief connection in Eo-Oligocene time (?40–?35 m.y. BP; Berggren & Van Couvering, 1974), Europe and Africa were rejoined about 18 m.y. BP (Cooke, 1972; Hallam, 1973; Dewey *et al.*, 1973; Berggren & Van Couvering, 1974). The nature and extent of the direct Late Cretaceous and Paleogene connections between Europe and Africa, affected greatly by epicontinental seas, need further investigation. At any rate, it is evident that some groups of angiosperms (*e.g.*, Fagaceae, Bombacaceae; Wolfe, this symposium), vertebrates (*e.g.*, marsupials; Lillegraven, 1974), and invertebrates (*e.g.*, mayflies of the family Siphlonuridae; Edmunds, this symposium), did pass between the Northern and Southern Hemispheres at these times, and the connection between Africa and Europe was certainly more direct than either that between North and South America or that between Asia and Australia until at least the Late Miocene. The extent to which India might have provided a bridge between northern and southern lands as it moved northward remains a fascinating question.

Northern Hemisphere Migration Routes

From the time of Asa Gray a century ago, it has generally been assumed that migration between Eurasia and North America took place largely through the Bering Straits area and was controlled mainly by climate. It is now clear, however, that this picture is imprecise. Land connections existed across the North Atlantic in Cretaceous and Paleogene time, and were direct until approximately 49 m.y. BP (McKenna, this symposium). Plants have continued to disperse across the North

Atlantic until the present because the water gaps are not extant in this area, and the climate has become unfavorable for most plants only in the Late Pliocene. The cessation of most migration by mammals across the North Atlantic about 49 m.y. BP, contrasting with the continued Trans-Atlantic establishment of plants, clearly is related to the different dispersal capabilities of the two groups.

In the Cretaceous and Early Tertiary, the epicontinental Turgai Straits sea barrier was a barrier to migration between most of Eurasia and North America. Furthermore, easternmost Asia is geologically a part of the North American plate, and became joined with the mainland of Asia only about 70 m.y. BP. Not until the Turgai Straits dried up in the Oligocene did patterns of migration around the Northern Hemisphere exist in essentially their modern configuration (McKenna, this symposium). In addition, North America was divided in two parts by epicontinental seaways extending from the Arctic Ocean to the Gulf of Mexico during the last two-thirds of the Cretaceous (Lillegraven, 1974: 269–270). The mammal fauna of eastern Asia was highly endemic from the Cretaceous until the Oligocene, when direct connections with Europe were established, and the Early Eocene mammals of Europe are much more like those of North America (34 of 60 genera in common) than those of Asia (only 2 of 60 genera, both abundant in North America and probably reaching Asia via Beringia). For both mammals and dinosaurs, Late Cretaceous migration between Asia and North America seems to have been a rare event, suggesting sweepstakes dispersal (Kielan-Jaworowska, 1975).

The botanical data, on the other hand, appear to contrast with those derived from the vertebrates. Wolfe (this symposium) has pointed out that in the Late Cretaceous, there were two distinctive Northern Hemisphere provinces as defined by palynology, one (the Normapollenites flora) including eastern North America and Europe and a second (the Aquilapollenites flora) including the major part of Asia and western North America. The existence of the latter is explicable only by the greater dispersal capacities of plants than vertebrates, and the constituents of the Aquilapollenites flora supposedly characteristic of both areas need to be examined in detail. Perhaps this palynological province is defined to a greater extent by the nearly complete absence of the Normapollenites constituents characteristic of Europe and eastern North America than by a great number of pollen genera common to Asia and western North America in Late Cretaceous time. The geological basis for a sharp division in the Late Cretaceous between eastern and western North America has just been mentioned. Be that as it may, there were relatively direct opportunities for migration between western North America and Asia from 70 m.y. BP onward, and some warm-temperate plants certainly migrated between North America and Eurasia in Late Cretaceous and Paleogene time, either via Beringia or via the North Atlantic region (where few plant fossils of this age have yet been reported). Wolfe (this symposium) has properly stressed the role of the Indomalayan region as a center for survival of formerly more widespread Northern Hemisphere tropical to subtropical plants, as pointed out earlier by Thorne (1965) and others.

Patterns of migration that are geologically more recent have been discussed

by Savile (this symposium), who has studied the coordinated evolution of Saxifragaceae s. str. and their associated rust fungi to derive a detailed picture of migration through Beringia. Most of this dispersal seems to have taken place in Neogene time and more recently, and it serves to underscore the virtual continuity between eastern Asia and North America throughout this period.

Tertiary Aridity in the Southeastern United States

During the Eocene and Oligocene, semiarid climates evidently developed in the southeastern United States, as stressed both by Axelrod and by Wolfe in this symposium. Some sclerophyllous or otherwise drought-adapted plants may have dispersed between Europe and North America via a narrower North Atlantic at these times, although there are few links between the vegetation of the Mediterranean region and North America that cannot be explained by convergent evolution from more mesophytic ancestors (Raven, 1973). The existence of such climates in Paleogene time likewise may be related to the survival of certain xerophytic communities in the southeastern United States, as stressed by Axelrod (this symposium).

Appalachian and Mexican-Central American Disjunctions

In Paleogene times, a nearly continuous warm temperate to subtropical forest occurred over much of North America, excluding the far north and zones of aridity in the southeastern United States and the area of northwestern Mexico (Axelrod, this symposium). This forest was much richer in genera and species than any of its local derivatives which persist at present. Many of the disjunctions between the Appalachians and the mountains of Mexico and Central America seem now to have come about when spreading aridity interrupted what was probably originally a broad belt of warm temperate to subtropical vegetation extending from much of the United States southward through the older Sierra Madre Occidental of Mexico to northern Central America. Many of the genera were eliminated from this forest in the western United States and northern Mexico in Neogene times and more recently by drought at low-middle latitudes, but others survived following their spread eastward into the Sierra Madre Oriental as these mountains were raised up from the Miocene onward. Thus there is no need to postulate direct migration of many of the forest elements between the Appalachians and the mountains of southern Mexico-Central America, although relatively long-distance dispersal has evidently added to the lists of disjunct species and genera relatively recently.

Role of Biology in Interpreting Geological Evidence

Earlier, when the geological evidence was less clear, analyses of the ranges of plants and animals contributed useful hypotheses about past geological events. This was, of course, especially true when these connections represented the sort of vacariant relationships discussed so ably by Cracraft (this symposium). Now, however, geology has arrived at a degree of sophistication where biologists must pay more attention to that evidence, to the age of their groups, and begin to

integrate them into more realistic patterns. If the biological evidence, independently evaluated, suggests serious discrepancies with the geological evidence, then the latter should obviously be re-examined. In a case like that discussed by McKenna (this symposium) for mammal ties between the northern continents, biological evidence is so strong that if the geological evidence suggested that there was no direct land connection across the North Atlantic it would certainly seem implausible. In the geologically poorly understood area of Africa-India-Madagascar, Edmunds (this symposium) has suggested that biology strongly supports a connection which persisted between India-Madagascar at a time when there was no direct connection of Madagascar with Africa. He has presented powerful arguments for letting the biological evidence speak for itself, following comprehensive study of the organisms concerned in the field and in the laboratory. Savile (this symposium) has shown very clearly how interacting systems involving plants and parasites, or host–parasite relationships, can be used to evaluate biogeographical relationships in an even more precise way, and Schlinger (1973) and others have provided other useful examples, especially in connection with the *Nothofagus* forests.

Many new interpretations of the distribution of organisms will be possible in the future as geological evidence continues to accumulate and be further refined, but particularly as new evidence of fossil floras continues to accumulate, and as older studies are critically revised. For example, it would be possible to chart the distribution and spread of the various groups of *Nothofagus* without knowledge of the fossil record. However, the extinction of the *menziesii* and *brassii* groups in Australia and New Zealand could not have been predicted, and erroneous conclusions about differing migration routes or "tracks" from New Zealand into South America might well be deduced from the evidence of existing species alone. However, the sort of connection between New Guinea and New Caledonia, suggested by Cracraft (this symposium) on the basis of the existence of living species, illustrates the trap into which one can enter without reference to fossil evidence, for the geology of New Guinea and the lands outside the spreading basins (Fiji, New Caledonia) to the east suggest something quite different. Since the *brassii* group of *Nothofagus* was widespread in Australia into Early Pleistocene time and became extinct only within the last million years, it is uncritical to assert that the existence of the *brassii* group in New Guinea and New Caledonia provides any evidence of former land connections between these areas, for which there is quite another explanation (Raven & Axelrod, 1972). Clearly, our increasing knowledge of the fossil record of this genus (*e.g.*, Archangelsky & Romero, 1974), will eventually make possible an even more accurate knowledge of its pathways of migration than we have at present.

As increasingly critical phylogenetic interpretations are made for various groups (Cracraft, this symposium), more geological evidence accumulates, and the fossil record becomes better and better known, we shall clearly continue to move toward a stronger, more enlightened synthetic theory of biogeography. The papers presented in this symposium provide ample evidence of the vitality of this venerable field of human investigation.

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WOOD ANATOMY OF ONAGRACEAE, WITH NOTES ON ALTERNATIVE MODES OF PHOTOSYNTHATE MOVEMENT IN DICOTYLEDON WOODS[1]

SHERWIN CARLQUIST[2]

ABSTRACT

Vessel elements in Onagraceae correlate perfectly with groups of species; elements are long and wide in mesomorphic species, shortest and narrowest in the most xeromorphic species. Libriform fibers in the family are thin-walled, but many have gelatinous inner walls. The possibility that these represent not tension wood but a water-storage mechanism is examined. Libriform fibers are mostly septate or nucleate or both in the family; this indicates longevity and simulation of parenchyma in starch-storage function. These fibers may compensate for the paucity of axial parenchyma. Interxylary phloem ("included phloem") does not occur in *Fuchsia*, *Hauya*, and *Ludwigia*, the genera in the family most generalized in other respects, and is absent in most annuals studied. Selective pressure for formation of interxylary phloem in the three genera may be minimal because of slow rates of photosynthate translocation within wood and selective pressure for formation of interxylary phloem in annuals may be minimal for spatial reasons. Interxylary phloem may be related to massive flowering that draws rapidly on stored starch, chiefly in the shrubby perennials. The relationships of Onagraceae seem closest to Lythraceae, Sonneratiaceae, Punicaceae, Crypteroniaceae, and Combretaceae; also close are other myrtalean families: Melastomaceae, Myrtaceae, Penaeaceae, Oliniaceae. These affinities are clearly evident from wood features alone: vestured pits on vessels; ray cells upright to square; intraxylary phloem present adjacent to pith; libriform fibers septate or nucleate; prismatic crystals in fibers and rays. Onagraceae tend to show herbaceous characteristics in wood of herbaceous genera; woody genera such as *Hauya* show no indicators of herbaceous structure. The ancestral habit of Onagraceae was probably shrubby, and without interxylary phloem; interxylary phloem may have evolved more than once in the family.

A practical but compelling reason for presenting this study at this time is the availability to me of an exceptional collection of wood samples. Numerous Onagraceae have woods with technically important features: interxylary phloem and associated thin-walled cells; nucleate fibers; and starch in various cell types. These features are present in or can be studied adequately only in liquid-preserved material. Dr. Peter H. Raven appreciated these facts and assembled a very fine basic collection of liquid-preserved wood samples of Onagraceae over a period of years. He has kindly placed this collection at my disposal. Although additional wood samples have been incorporated in this investigation, the Raven collection, which represents the work of Dr. Raven and Dr. Dennis E. Breedlove (see Table 1) provided an unusual opportunity and a pleasant challenge for understanding of wood structure. Probably no other study on wood anatomy of dicotyledons has been based on such a high proportion of liquid-preserved samples. The usual assumption by wood anatomists is that little of value is lost when wood samples are prepared by drying. Even if this is true in many families, it clearly is not in certain others.

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The nature of cells related to photosynthate conduction in wood has been poorly appreciated, yet Onagraceae proves a key group in comprehending this phenomenon. Only recently have beginnings been made, as the works by Braun (1970) and Wolkinger (1969, 1970, 1971) demonstrate. I have attempted to integrate concepts of photosynthate translocation and storage into a hypothesis of xylem evolution (Carlquist, 1975) that stresses the preliminary and tentative nature of our knowledge.

However, Onagraceae are a group of exceptional interest with respect to wood anatomy for other reasons as well. Growth forms in this family range from small annual herbs to large annual and biennial herbs; from subshrubs to large shrubs; and even to medium-sized trees (*Hauya*, *Fuchsia*). A family with this range of growth forms and with a high proportion of herbs or woody herbs deserves special attention because our knowledge of characteristics of wood of herbs and herb-like plants is still quite inadequate. We do not know whether wood anatomy can be decisive in discerning direction of phylesis from woody to herbaceous or the reverse. Onagraceae is obviously a strategic family in this regard. The question of whether Onagraceae as a whole are primitively woody or herbaceous has not been answered, nor do we have any well-supported concepts of which tribes of the family represent phylesis to or from woodiness or herbaceousness.

In addition, only a small proportion of woods in the family have been studied by wood anatomists, as the account of Metcalfe & Chalk (1950) shows. This lack derives from the fact that, most frequently, wood of tree species has formed the basis for wood collections and these collections in turn, formed the basis for studies by wood anatomists. Obviously we cannot fully understand the nature of wood anatomy in tree species without broadly-based comparisons with wood of non-arboreal families, genera and species.

Materials and Methods

The liquid-preserved collection of wood samples prepared by Peter H. Raven and Dennis E. Breedlove, mentioned above, consisted of portions, many from bases of plants, pickled in formalin-acetic alcohol. Also present among the wood assemblage were dried wood samples (*Ludwigia octovalvis*, *Raven 18670*; logs of *Hauya elegans* subsp. *cornuta*, *Breedlove 6432* and *10589*). Dried wood samples of *Fuchsia fulgens* and *F. parviflora* were kindly provided by Dr. Hugh H. Iltis. My wood sample of *F. cyrtandroides* was dried. All these wood samples are related to voucher specimens, as indicated in Table 1. No voucher specimen, however, was collected for *Lopezia miniata* subsp. *paniculata* by Robert Dressler. However, other specimens of this population, such as *Allen 987* (MO) can be cited as documenting the identity of these plants from Chiriquí, Panama (Peter H. Raven, personal communication).

Wood samples from six specimens of *Fuchsia* in the University of California Botanical Garden, Berkeley, augment the collection. Sizeable stems of these specimens, mostly basal portions, were collected with the permission of Dr. Robert Ornduff. During December, 1972, a severe freeze killed these and other plants to the ground or nearly so. The stems were taken and pickled on December 25,

1972, before histological deterioration occurred. Accession numbers of these *Fuchsia* plants at the Botanical Garden are indicated in Table 1; no voucher specimens exist. A liquid-preserved wood sample of *Zauschneria cana* (voucher in RSA) was prepared from a shrub approximately eight years old at the Rancho Santa Ana Botanic Garden.

A few collections could not be studied with respect to wood anatomy because grain of wood proved excessively twisted, because stems were too small, or because pickled material had dried. Most woods of Onagraceae are relatively soft. Because of this or small size, a few had to be embedded in paraffin and sectioned on a rotary microtome. The vast majority, however, were sectioned on a sliding microtome; these sections range between 18 and 26μ in thickness. In each collection, I selected the largest stems in order to present the most mature wood pattern. However, wood of relatively small stems in annuals and biennials can be expected to be different from that of a tree, such as *Hauya*. Changes during ontogeny were noted, as in the rays of *Hauya* (Figs. 8–10).

Some sections were stained with safranin only. However, counterstaining with haematoxylin or Fast Green proved valuable for improved visibility of phloem strands and associated thin-walled parenchyma. Sections counterstained with Fast Green tend to show differential staining of gelatinous fibers: the outer portions of secondary walls stain red because of lignification, whereas the inner non-lignified portions stain green. This can be seen clearly in Fig. 33. Polarizing apparatus was used during examination of wood sections to detect presence of crystals and starch. Some photographs were made under polarized light employing various degrees of crossing of the nicol elements. Non-polarized light was used for photographs unless otherwise stated.

In the photographic figures, wood transections are oriented with outer (toward cambium) portion of wood upward unless otherwise indicated. If only one collection of a species or infraspecific entity was studied, the collection is not mentioned in the figure legend, but is cited in Table 1. Where more than one collection of an entity was studied, the photographed section is identified by collection number in the figure legend. Authors of binomials are cited in Table 1, and not used elsewhere in this paper.

Tabular Data.—Table 1 lists species according to tribes. These tribes and their generic content agree basically with the scheme of Raven (1964). However, because of its distinctive wood features, I have listed *Hauya* within the tribe Hauyeae, as did Munz (1965) and Kurabayashi, Lewis & Raven (1962). Raven (1969) may well be correct in his reasons for including *Hauya* within Onagreae. I have isolated Hauyeae and placed it at the end of Table 1 for convenience in comparing wood features; this placement does not represent a taxonomic or phylogenetic judgment.

Ludwigia is used in the sense of Raven (1962, 1963). *Calylophus* and *Camissonia* are employed in agreement with Raven's (1964, 1969) concepts. *Gongylocarpus* includes *Burragea*, as in Carlquist & Raven (1966). Because the Carlquist and Raven paper incorporated photographs, only tabular data on *Gongylocarpus* is included in the present paper. Treatment of the tribe Lopezieae

is in accordance with that of Plitmann, Raven & Breedlove (1973). Those authors have reduced *Diplandra*, *Jehlia*, *Pseudolopezia*, and *Semeiandra* to sections of the genus *Lopezia*, which thereby becomes the sole genus of the tribe. The species studied here belong to sections or former segregate genera as follows: *Diplandra* (*L. lopezioides*); *Pseudolopezia* (*L. longiflora*); *Riesenbachia* (*L. riesenbachia*); *Semeiandra* (*L. semeiandra*). The remaining species of Lopezieae studied here were treated within the genus *Lopezia* prior to the treatment of Plitmann, Raven & Breedlove (1973). Breedlove and Raven are publishing new combinations in *Hauya*, and one of these is utilized for Hauyas studied here.

Table 1 offers quantitative data as well as qualitative data on features where a range or expressions or significant differences exist. Additional characteristics, and lists of species in which these were observed, are cited in the text. Quantitative data in Table 1 are self-explanatory. They were based on fifty measurements per feature for each species unless fewer measurements were made in instances where a particular feature was scarce on slides. Rays of particular types were scarce on slides of some species, particularly those with small stems, and where only a very limited (and therefore meaningless) number of measurements could be made, quantitative data are omitted in Table 1.

Vessel Elements

Vessel-Element Dimensions and Their Significance.—Quantitative data on vessel elements cannot be reliably interpreted on the basis of individual species: variations of any given specimen and the chances of obtaining unrepresentative measurements make this procedure not feasible. For this reason, the data in Table 1 have also been summarized as averages for the following six groups of species: Fuchsieae; Lopezieae that are shrubs; Lopezieae that are annuals or suffrutescent perennials; Onagreae that are annuals (or winter biennials); Onagreae that are perennials, sprouting from a woody caudex; and Hauyeae, all of which are trees. The ecological significance of these categories is as follows: Hauyeae are small to medium-sized trees of moist to somewhat seasonal tropical forests, tending to be upland elements rather than coastal. Hauyeae probably transpire large volumes of water when humidity is low, judging from the large size of their leaves. However, soil moisture is probably nearly always available to them. Fuchsieae likewise characteristically inhabit moist habitats, either in cool subtropical uplands, closer to sealevel in temperate latitudes or, if in temperate uplands, relatively free from frost. Both Hauyeae and Fuchsieae are mesophytes, with minimal seasonality for the family. The larger shrubby Lopezieae tend to have thick, rather succulent stems and to grow in the understory of subtropical upland forests of Mexico. These forests experience a dry season, but have less limited moisture supplies than exposed sites. The annual and suffrutescent Lopezieae do often grow in exposed sites; some species in this group are facultative annuals that may persist into a second season and thus are more exposed to water stress during summer drought than are Lopezieae in shadier, moister localities. Water stress, and the accompanying negative pressures in vessels, ought to be less in these Lopezieae than in the Onagreae that are caudex perennials; these Onagreae are temperate herbs (*e.g.*,

TABLE 1. Wood characteristics of Onagraceae.—The numbers corresponding to characteristics are: 1. Vessel element length, average, μ. 2. Vessels per mm², average. 3. Vessels per group, average. 4. Vessel diameter, average, μ. 5. Libriform fiber length, average, μ. 6. Length ratio of libriform fibers to vessel elements. 7. Multiseriate ray width, average, cells. 8. Multiseriate ray height, average, cells. 9. Uniseriate ray height, average, cells. 10. Ray histology. 11. Libriform fibers. 12. Interxylary phloem. 13. Tyloses. 14. Starch. 15. Raphides.

Taxon	Collection	Characteristics (see table caption)														
		1	2	3	4	5	6	7	8	9	10[a]	11[b]	12[c]	13[d]	14[e]	15[f]
Tribe Fuchsieae.																
Fuchsia boliviana Britton	*UCBBG 49.815*	363	48	2.1	74	550	1.50	2.8	15	4.8	Usp	S	0	+	0	0
F. cyrtandroides J. W. Moore	*Carlquist 653* (RSA)	440	20	1.2	103	462	1.40	3.8	11	3.0	USp	S	0	+	0	0
F. fulgens DC.	*Iltis et al. 844* (MAD)	299	52	2.2	87	621	2.08	2.5	17	4.6	U	S	0	0	0	F
F. lycioides Andr.	*UCBBG 53.1303*	286	50	1.9	58	462	1.60	3.0	12	4.5	Us	S	0	+	0	F
F. magellanica Lam. var. *globosa* (Lindl.) Bailey	*UCBBG 49.808*	385	48	2.2	84	561	1.46	6.0	22	4.2	Us	S	0	+	0	F
F. magellanica var. *macrostemma* (R. & P.) Munz	*UCBBG 49.806*	352	44	1.8	61	517	1.47	2.7	14	4.5	USp	S	0	+	0	F
F. paniculata Lindl.	*Breedlove 7145* (DS)	550	22	1.5	86	770	1.40	2.9	15	5.0	Usp	S	0	0	0	0
F. parviflora Lindl.	*Iltis et al. 846* (MAD)	471	124	1.9	64	824	1.75	2.8	22	3.3	Us	S	0	0	0	0
F. splendens Zucc.	*Raven 7796* (DS)	462	54	1.4	69	649	1.40	—	—	13	Us	S	0	+	F,R	0
F. tincta I. M. Johnston	*UCBBG s.n.*	330	50	2.0	54	473	1.45	2.7	24	4.5	Us	S	0	+	0	0
F. tuberosa Krause	*UCBBG 48.817*	324	180	1.4	39	440	1.35	2.6	20	3.2	U	S,N	0	+	P	0
Fuchsieae combined		387	61	1.8	71	575	1.69	3.1	17.3	5.0						
Tribe Lopezieae																
Lopezia grandiflora Zucc.	*Breedlove 7182* (DS)	347	53	1.5	62	451	1.30	2.0	8.0	3.0	Usp	N,S	S	0	F	0
L. langmaniae Miranda	*Breedlove 7161* (DS)	385	30	1.2	62	484	1.24	—	—	2.8	Usp	N	B	0	0	0
L. longiflora (Decaisne) Plitmann, Raven & Breedlove	*Breedlove 8044* (DS)	319	19	1.5	110	484	1.51	—	—	3.7	USP	N	B	0	F,P	0
L. lopezioides (H. & A.) Plitmann, Raven & Breedlove	*Breedlove 7268* (DS)	451	32	1.7	64	638	1.41	2.0	8.0	6.0	USp	N	B	+	F,P	P
L. lopezioides (H. & A.) Plitmann, Raven & Breedlove	*Breedlove 8052* (DS)	314	26	2.5	77	451	1.43	2.1	12	5.2	uSp	N	B,S	+	F,P	P
L. miniata Lag. ex DC. subsp. *miniata*	*Breedlove 4244* (DS)	297	86	1.5	54	429	1.40	2.0	6.2	3.2	Usp	N	B,S	+	0	0
L. miniata subsp. *paniculata* (Seem.) Plitmann, Raven & Breedlove	*Dressler* (no voucher)	363	47	1.4	57	532	1.47	2.0	22	7.4	uSp	S,N	S	0	F,R	P
L. racemosa Cav. subsp. *moelchenensis* Plitmann, Raven & Breedlove	*Breedlove 6971* (DS)	270	156	2.1	51	377	1.40	2.2	5.0	2.1	Us	N	S	+	F	P
L. racemosa subsp. *racemosa*	*Breedlove 7030* (DS)	275	69	1.4	59	341	1.29	2.0	5.7	2.3	Usp	N	S	0	F	0
L. riesenbachia Plitmann, Raven & Breedlove	*Breedlove 8071* (DS)	338	112	1.9	52	508	1.50	2.4	7.0	3.0	Us	N	0	0	F	0
L. semeiandra Plitmann, Raven & Breedlove	*Breedlove 8061* (DS)	385	25	1.5	92	506	1.32	2.0	7.7	3.8	Usp	S,N	S	0	F	P
Lopezieae: shrubs combined		356	30	1.7	81	506	1.39	2+	8.9	4.3						
Lopezieae: annuals, suffrutescent perennials combined		321	83	1.6	56	445	1.38	2.1	9.2	3.4						

[a] Symbols used: cells upright (U), square (S), or procumbent (P); upper case letters indicates which of the three types predominates; *e.g.*, "Us" denotes presence of numerous upright ray cells, some square ray cells and no procumbent ray cells.

[b] Symbols used: libriform fibers nucleate (N), septate (S), or neither characteristic present (0).

[c] Symbols used: phloem cells present in secondary xylem within tangentially-widened bands (B), within narrow strands (S), or absent (0).

[d] Symbols used: tyloses observed (+), or not seen (0).

[e] Symbols used: starch grains observed in libriform fibers (F), in parenchyma associated with phloem in interxylary phloem bands (P), in ray cells (R), or absent in wood (0).

[f] Symbols used: idioblastic cells bearing crystals occur in fiber-like cells of the fascicular xylem (F), in parenchyma of the interxylary phloem (P), in ray cells (R), or are absent in wood (0).

TABLE 1. (continued)

Taxon	Collection	Characteristics (see table caption)														
		1	2	3	4	5	6	7	8	9	10[a]	11[b]	12[c]	13[d]	14[e]	15[f]
Tribe Onagreae																
Calylophus hartwegii (Benth.) Raven subsp. *pubescens* (Gray) Towner & Raven	*Raven 19202* (DS)	185	271	1.4	37	302	1.63	—	—	—	Us	N	B	0	F	0
C. serrulatus (Nutt.) Raven	*Raven 19034* (DS)	136	460	2.1	59	242	1.78	—	—	1.5	U	S,N	B,S	0	F	0
Camissonia californica Raven	*Raven 20172* (DS)	308	78	2.1	59	440	1.41	2.0	8.8	7.8	U	N	0	0	0	0
C. cheiranthifolia (Hornem. ex Spreng.) Raimann	*Raven 20161* (DS)	165	129	2.2	54	286	1.77	—	—	3.5	U	N	B,S	0	F	0
C. megalantha (Munz) Raven	*Beatley* in 1962 (DS,RSA)	407	69	1.7	57	486	1.44	2.0	9.6	6.0	Usp	N	S	0	I	0
Clarkia xantiana (Gray)	*Raven 20254* (DS)	341	130	2.7	46	451	1.33	2.2	11.5	2.7	uSp	N	0	0	F,R	0
Gaura biennis L.	*Raven 19661* (DS)	264	100	3.0	66	451	1.73	2.0	16	10	Usp	0	B,S	0	0	0
G. longiflora Spach	*Raven 19396* (DS)	341	72	1.7	79	467	1.36	2.0	23	12	uSp	N	S	0	0	F
G. parviflora Dougl.	*Raven 19573* (DS)	236	70	2.4	79	285	1.64	2.0	18	4.1	Us	N	S	0	0	0
G. sinuata Nutt. ex Sér.	*Raven 19198* (DS)	106	320	1.7	46	305	2.88	—	—	—	Usp	S,N	B,S	+	P	F,P
G. villosa Torr. subsp. *villosa*	*Raven 19224* (DS)	257	114	1.5	59	540	2.10	2.9	11.1	4.3	uSp	N	S	0	I	I,F,R
Gongylocarpus fruticulosus (Benth.) Brandegee subsp. *glaber* (Thomas) Carlquist & Raven	*Moran 10810* (DS)	226	62	2.0	33	400	1.33	2.8	11.5	3.1	USp	N	S	+	R	I
G. rubricaulis Schlecht. & Cham.	*Breedlove 7154* (DS)	361	84	1.9	63	490	1.35	2.3	12.5	3.2	Usp	0	0	0	0	0
Heterogaura heterandra (Torr.) Cov.	*Raven 20238* (DS)	286	77	2.4	53	374	1.30	—	—	—	Us	N	0	0	0	0
Oenothera crassifolia Greene	*Raven 17024* (DS)	209	276	1.8	35	319	1.54	2.2	10.8	3.9	USp	N	B	+	0	0
O. deltoides T. & F. subsp. *howellii* (Munz) Klein	*Raven 20181* (DS)	292	72	2.9	58	352	1.20	2.0	5.3	1.9	Us	N	B,S	0	0	P
O. drummondii Hooker	*Raven 19392* (DS)	229	80	1.4	59	363	1.58	2.0	4.4	2.2	Usp	N	S	+	0	P
O. elata H.B.K.	*Raven 8042* (DS)	297	62	2.8	74	462	1.58	—	—	—	Us	N	S	0	0	0
O. linifolia Nutt.	*Raven 19450* (DS)	242	246	2.9	49	385	1.59	2.0	12.2	5.6	Usp	N	B,S	0	0	F,P
Xylonagra arborea (Kell.) Donn. Smith & Rose subsp. *wigginsii* Munz	*Thomas 8215* (DS,RSA)	187	41	1.7	69	308	1.63	3.2	15.6	2.4	Us	N	B	0	F	P,R
Onagreae: annuals combined		299	111	2.4	60	430	1.46	2.1	12.8	5.6						
Onagreae: caudex perennials combined		189	218	1.7	49	359	1.88	2.5	9.0	3.2						
Tribe Jussiaeeae																
Ludwigia octovalvis (Jacq.) Raven	*Raven 6571* (DS)	429	90	1.5	66	611	1.42	4.0	59	2.6	Us	S,N	0	+	F	0
L. octovalvis (Jacq.) Raven	*Raven 18670* (DS)	544	85	1.1	57	813	1.49	2.8	41	4.0	Us	S,N	0	+	F	0
L. uruguayensis (Cambess.) Hara	*Thomas 7219* (DS)	356	48	1.2	74	700	1.97	2.3	34	8.0	Usp	N	0	0	F,R	0
Tribe Epilobieae																
Epilobium paniculatum Nutt. ex T. & G.	*Raven 20668* (RSA)	235	104	2.1	54	342	1.46	2.1	10	7.2	Us	N	0	0	F	0
Zauschneria cana Greene	*RSABG 13577*	151	360	1.6	41	309	2.05	2.4	2.7	2.3	Us	N	B,S	0	F	0
Tribe Hauyeae																
Hauya elegans DC. subsp. *cornuta* (Hemsl.) Raven & Breedlove	*Breedlove 6432* (DS)	415	30	1.7	96	730	1.76	2.2	8.4	4.3	usP	N	0	0	F,R	F
H. elegans subsp. *cornuta*	*Breedlove 10589* (DS)	341	29	1.9	98	814	2.41	4.8	15.6	2.9	usP	0	0	0	F	F
H. elegans subsp. *cornuta*	*Carlquist VI-1958* (RSA)	429	31	1.4	92	765	1.80	2+	9.3	6.2	USP	0	0	0	F,R	F
Hauyeae combined		395	30	1.7	95	770	1.99	3.0	11.1	4.5						

Gaura) that persist through dry summers. Annual Onagreae do not persist through summer drought and therefore would not be expected to have xylem adapted to high negative pressures in vessels. The above habit and habitat data are derived from Munz (1965), Plitmann, Raven & Breedlove (1973), and from my own observations.

I have hypothesized (Carlquist, 1975) that long, wide vessel elements are of adaptive value where soil moisture is abundant and transpiration relatively uniform because of relatively constantly high humidity; short, narrow vessel elements are adaptive in situations where periods of low soil moisture and low humidity create high tensions in vessel water columns. Succulence or seasonal loss of leaves would buffer the effect of these conditions. Detailed data basic to these concepts have been presented elsewhere (Carlquist, 1975) and cannot be repeated here. If correct, we would expect vessel dimensions for the six groups to fall in the following order:

Hauyeae (395 + 95 = 490)
Fuchsieae (387 + 71 = 458)
Lopezieae: large shrubs (356 + 81 = 437)
Lopezieae: annual and suffrutescent shrubs (321 + 56 = 377)
Onagreae: annuals (299 + 60 = 359)
Onagreae: caudex perennials (189 + 49 = 238)

The figures in parentheses represent average vessel element length, average vessel diameter (see Table 1), and the sum of these two dimensions. While either length or diameter is a reasonably accurate indicator of mesomorphy versus xeromorphy, the sum of the two is even more reliable. This sum, for example, was used for ranking the species of *Dubautia* (Carlquist, 1974: 153).

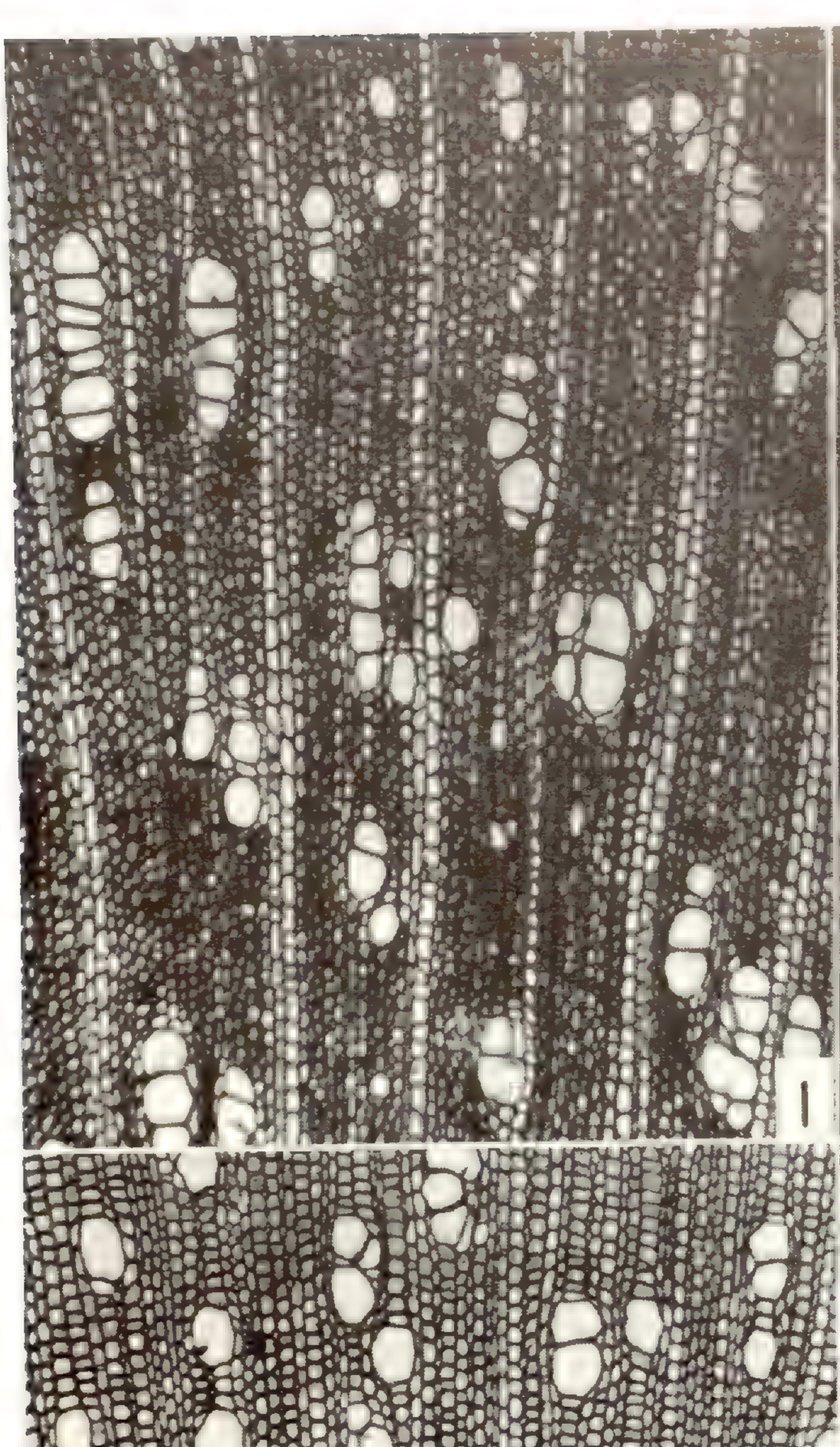
The accuracy of this means of ecological assessment can be demonstrated by figures for the Onagraceae not included within the above six groupings. For example, diameter plus length figures for *Zauschneria cana* (192), *Gongylocarpus fruticulosus* subsp. *glaber* (259) and *Xylonagra arborea* subsp. *wigginsii* (256) ought to fall close to the figure for caudex-perennial Onagreae, whose habit they simulate. The figures, as given in the parentheses beside each species, bear out this prediction. The Jussiaeeae, not calculated as a tribe in Table 1, have the following length plus diameter figures: *L. octovalvis* (495; 601); *L. uruguayensis* (430). Two of these figures exceed the figure for Hauyeae, which would seem to be paradoxical if Hauyeae represent mesic trees. However, only one condition can be said to be more moist than wet tropical forest: inundated soil. Jussiaeeae, in fact, can all be regarded as kinds of hydrophytes, so that the high figures obtained are understandable. Incidentally, I did not include hydrophytes in my 1975 survey of habit and habitat types in relation to xylem, because woody hydrophytes are neither numerous nor easily categorized. Thus, the hydrophytic Onagraceae add a new dimension to those results.

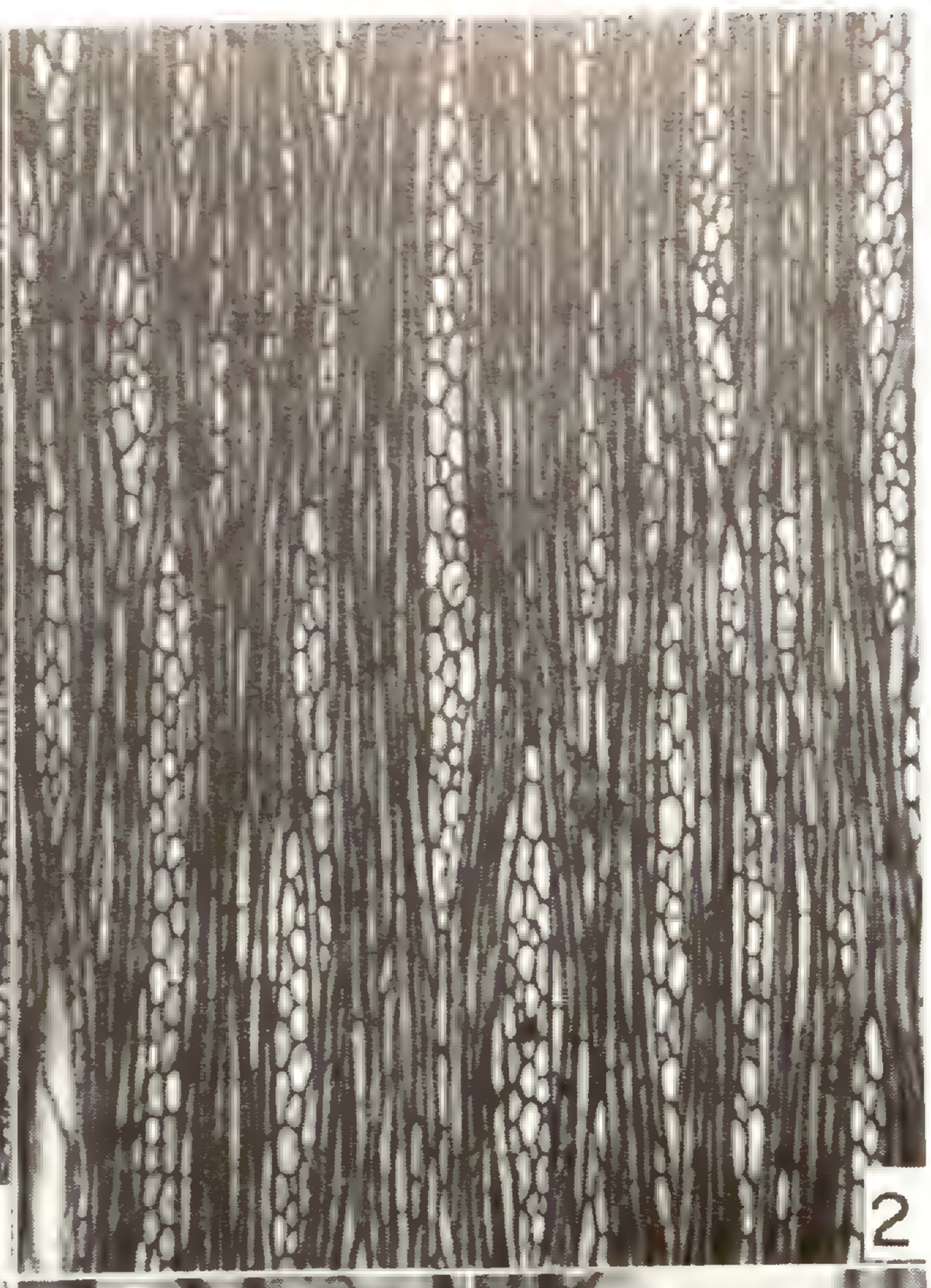
In my 1975 correlations, I demonstrated that narrowness of vessels in general is compensated for by more numerous vessels per unit transection. This can be seen clearly in the data of Table 1, especially in the average figures for the six

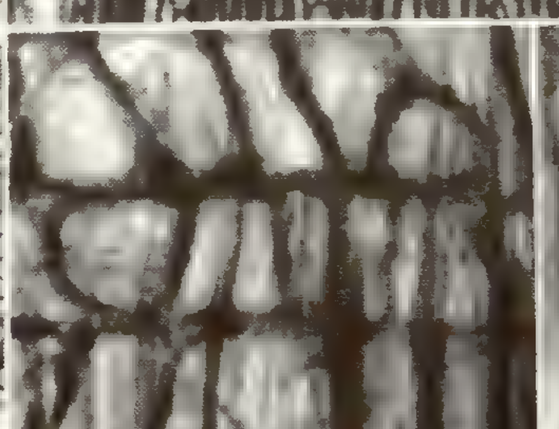
groupings mentioned above. One must remember that average area of vessels in transection, not merely diameter, is operative in these correlations. In addition, one may note that estimation of average number of vessels per square mm is very difficult, and where rather large numbers of vessels in a field, or a rather small number of vessels in a field occur, chances for unrepresentative figures are greater. If completely reliable measurements were available, a straight-line curve for vessels per square mm plotted against vessel diameter would probably result in Onagraceae, as in my 1975 book.

Vessel Groupings.—As can be seen from Table 1, the number of vessels per group does not fluctuate markedly in Onagraceae, in contrast to some families such as Asteraceae (Carlquist, 1966). In this respect, Onagraceae resemble such families as Goodeniaceae (Carlquist, 1969*a*) and Campanulaceae (Carlquist, 1969*b*). There appears to be little significance in this figure in Onagraceae, except for the annual Onagreae, which show a somewhat higher number of vessels per group. Larger groupings of vessels are illustrated here in one of these annuals, *Oenothera elata* (Fig. 34). The groupings that do occur can be characterized as forming radial chains or irregularly-clustered pore multiples. Radial chains tend to characterize the following species (in same order as in Table 1): *Fuchsia cyrtandroides*, *F. lycioides* (Fig. 1), *F. magellanica* var. *globosa*, *F. magellanica* var. *macrostemma*, *F. paniculata*, *F. parviflora*, *F. splendens* (Fig. 3), *F. tincta*, *F. tuberosa* (Fig. 49), *Lopezia langmaniae*, *L. miniata* subsp. *miniata* (Fig. 15), *L. miniata* subsp. *paniculata*, *L. racemosa* subsp. *racemosa* (Fig. 17), *L. riesenbachia*, *Camissonia californica* (Fig. 27), *Clarkia xantiana*, *Gaura parviflora*, *Oenothera elata* (Fig. 34), *Ludwigia octovalvis*, *L. uruguayensis* (Fig. 23), *Epilobium paniculatum*, and *Zauschneria cana*. Pore multiples are more typically found in *Fuchsia boliviana*, *F. fulgens*, *Lopezia grandiflora* (Fig. 14), *L. longiflora* (Fig. 19), *L. lopezioides* (Fig. 11), *L. racemosa* subsp. *moelchenensis*, *L. semeiandra*, *Calylophus hartwegii* subsp. *pubescens*, *C. serrulatus*, *Camissonia cheiranthifolia*, *C. megalantha*, *Gaura biennis*, *G. longiflora*, *G. sinuata*, *G. villosa* subsp. *villosa* (Fig 35), *Gongylocarpus fruticulosus* subsp. *glaber* (Carlquist & Raven, 1966), *G. rubricaulis*, *Heterogaura heterandra*, all species of *Oenothera* except *O. elata*, *Xylonagra arborea* subsp. *wigginsii* (Fig. 31), and *Hauya elegans* subsp. *cornuta* (Fig. 6). Obviously there is not much difference between these two modes of grouping when degree of vessel grouping is so low.

Vessel Shape.—As seen in transections, vessels in Onagraceae can be considered either round or angular in outline. Vessels round in outline characterize *Fuchsia boliviana*, *F. cyrtandroides*, *F. fulgens*, *F. lycioides* (Fig. 1). *F. magellanica* var. *globosa*, *F. magellanica* var. *macrostemma*, *F. parviflora*, *Calyophus serrulatus*, *Camissonia megalantha*, *Gaura biennis*, *G. sinuata*, *G. villosa* subsp. *villosa* (Fig. 35), all species of *Oenothera*, *Zauschneria cana*, and *Hauya elegans* subsp. *cornuta* (Fig. 6). Vessels tend to be angular in outline in *Fuchsia paniculata*, *F. splendens* (Fig. 3), *F. tincta*, *F. tuberosa* (Fig. 49), all species of *Lopezieae* (Figs. 11, 13, 15, 17, 19), *Ludwigia octovalvis*, *L. uruguayensis* (Fig. 23), and *Epilobium paniculatum*. Vessels angular in transectional view have traditionally been interpreted as primitive, but exceptions to this have been



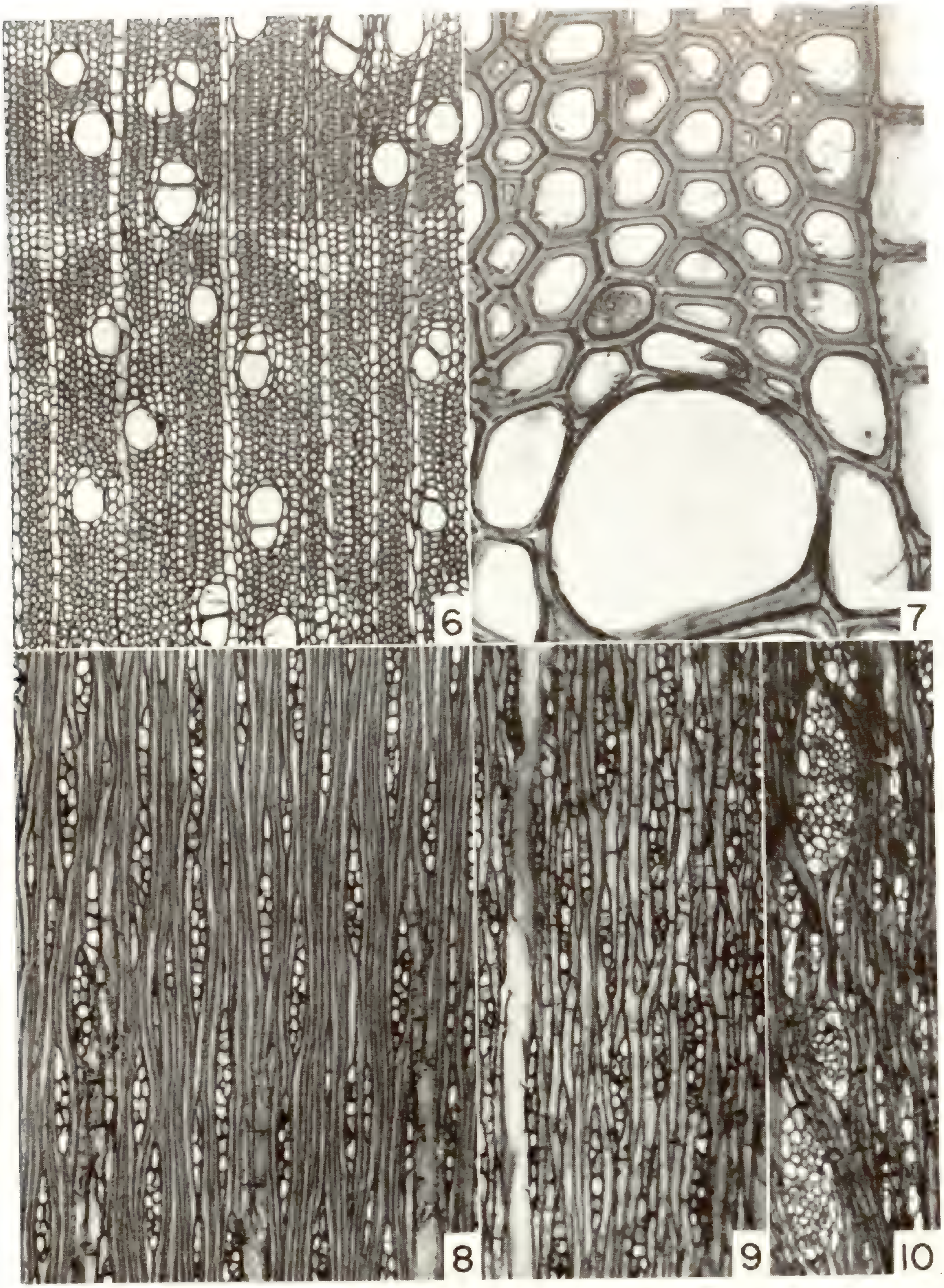




FIGURES 1–5. Wood sections of *Fuchsia*.—1–2. *F. lycioides*.—1. Transection. Darker zones are gelatinous fibers.—2. Tangential section. Rays are predominantly multiseriate.—3. *F. splendens*. Transection. Fibers notably thin-walled; a weak growth ring below.—4. *F. magellanica* var. *macrostema*. Portion of radial section showing a vertical pair of cells containing raphides.—5. *F. boliviana*. Portion of a radial section showing tyloses. [Magnification scale for Figs. 1–3 shown below Fig. 14; scale for Figs. 4–5 below Fig. 15.]

mentioned (Carlquist, 1962, 1969*b*). The reason for occurrence of angular vessels in primitive dicotyledonous woods is the tendency of these vessels to be narrow, with thin walls which therefore tend to follow the polygonal outlines of the grouping of few, rather wide tracheids that surround the vessels. This has been discussed more fully elsewhere (Carlquist, 1975). Circumstances like those in the primitive woods can occur in specialized woods also. If vessels are narrow and thin walled, yet libriform fibers are wide, vessel shape tends to be angular. Thin-walled vessels are likely to occur in woods in which strength of vessel walls is not high in selective value—a condition likely to occur in woods of herbs. Thus conditions predisposing to angularity of vessels are fulfilled in many Onagraceae. Both the thin-walled nature of vessels in many Onagraceae and the occurrence of rather wide, thin-walled short fibers connote a modest degree of mechanical strength.

Vestured Pits.—Onagraceae are notable for presence of vestured pits (Bailey, 1932, 1933). Vestured pits have wart-like intrusions of lignified wall material within pit cavities, as excellently demonstrated by means of electron microscopy of ultra-thin sections by Côté & Day (1962) and Schmid (1965). These authors did not study pits in Onagraceae, but did study them in genera of related myrtalean families: *Terminalia* (Combretaceae), *Eucalyptus* (Myrtaceae), and some Melastomaceae. Bailey (1933) is correct in saying that droplet-like deposits within pits can be mistaken for vesturing, and that therefore very thin sections are required for demonstrating true vesturing. Transmission electron microscopy has fulfilled this need more completely than Bailey could at that time have predicted. Scanning electron microscopy is also applicable, and vestured pits have been clearly figured by this means by Butterfield & Meylan (1973) for *Fuchsia excorticata* (J. R. & G. Forst.) L.f., a species not included in the present study. Careful observation by means of light microscopy of wood sections of entities in the present study revealed presence of vesturing in vessel pits, especially in the case of intervascular pitting. Vesturing is illustrated here for *Fuchsia paniculata* (Fig. 51), *Lopezia langmaniae* (Fig. 52), *L. lopezioides* (Fig. 53), *L. longiflora* (Fig. 54), and *L. miniata* subsp. *paniculata* (Fig. 55). However, little or no vesturing could be observed in vessel pits of *Oenothera deltoides* subsp. *howellii* (Fig. 56) or those of *Calyophus serrulatus*. Vesturing can be said to be vestigial in *Calylophus hartwegii* subsp. *pubescens*, the three species of *Camissonia* studied, *Oenothera drummondii*, *Fuchsia tuberosa*, *Gaura sinuata*, *Gongylocarpus fruticulosus* subsp. *glaber*, *Lopezia racemosa* subsp. *moelchenensis*, *Ludwigia uruguayensis*, and *Zauschneria cana*. Where pits are circular and relatively small, as in *Fuchsia paniculata* (Fig. 51), vesturing is most apparent along the slit-like pit apertures. Surprisingly, the wide pits of some lopezioids, in which pit apertures are notably broad (Figs. 52–53) show vesturing prominently. Because of the wide pit apertures, one may assume that the even granular appearance of the warts throughout the pit cavity means that warts are borne not just on the pit border, but on the pit membrane as well. This is evidently the case in a species from another family figured by electron microscopy by Côté & Day (1962), *Parashorea plicata* Brandis.



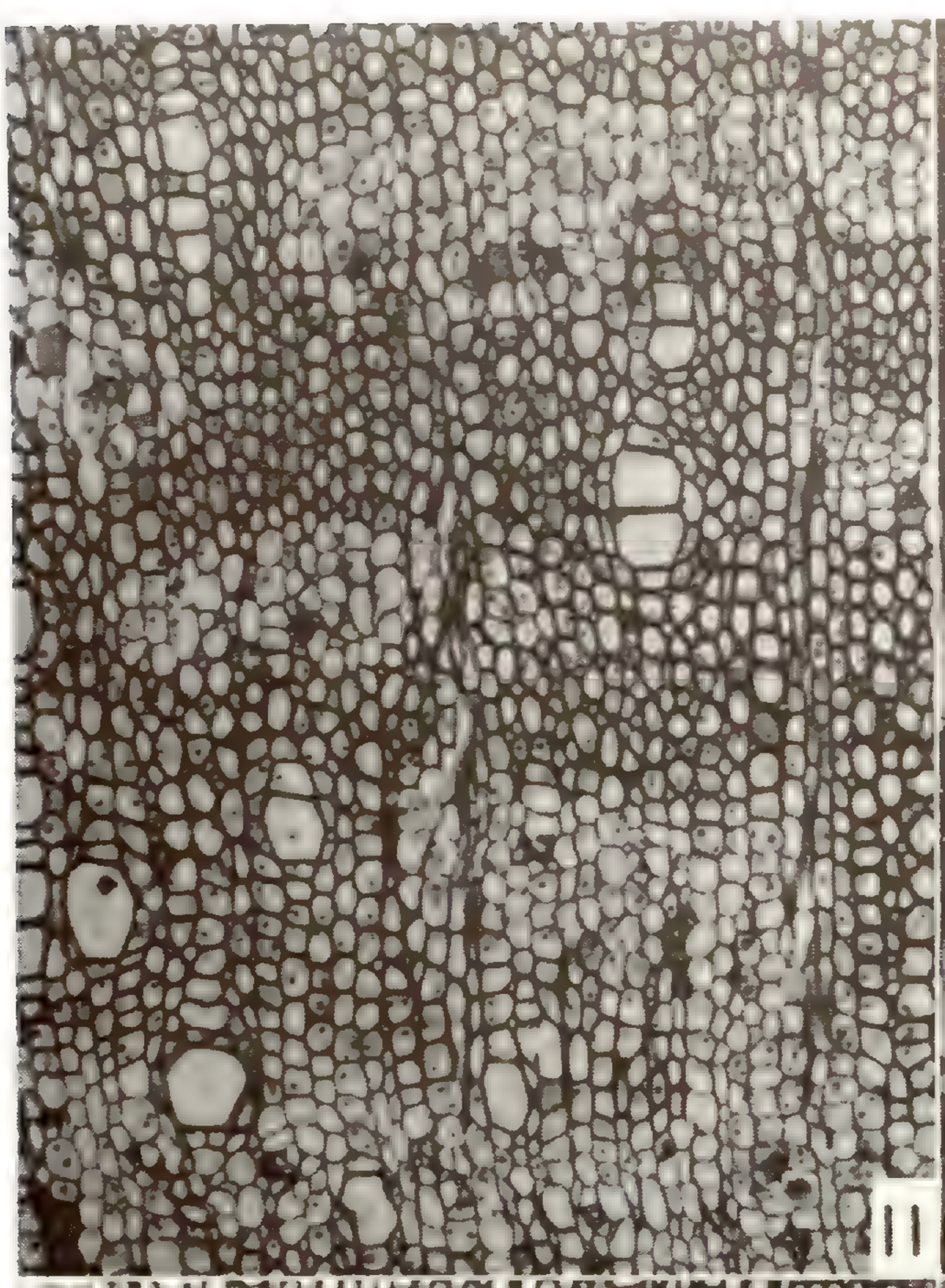
FIGURES 6–10. Wood sections of *Hauya elegans* subsp. *cornuta*.—6–9. *Breedlove 6432*.—6. Transection. Axial parenchyma cells form a band of variable width above center.—7. Portion of transection showing parenchyma cells around vessel; fibers above.—8–10. Tangential sections, from log 10 cm in diameter.—8. Zone with libriform fibers.—9. Another portion of the same section, showing an axial parenchyma band.—10. Section from a log 80 cm in diameter. *Breedlove 10589*. [Magnification scale for Figs. 6, 8–10 shown below Fig. 14; scale for Fig. 7 below Fig. 18.]

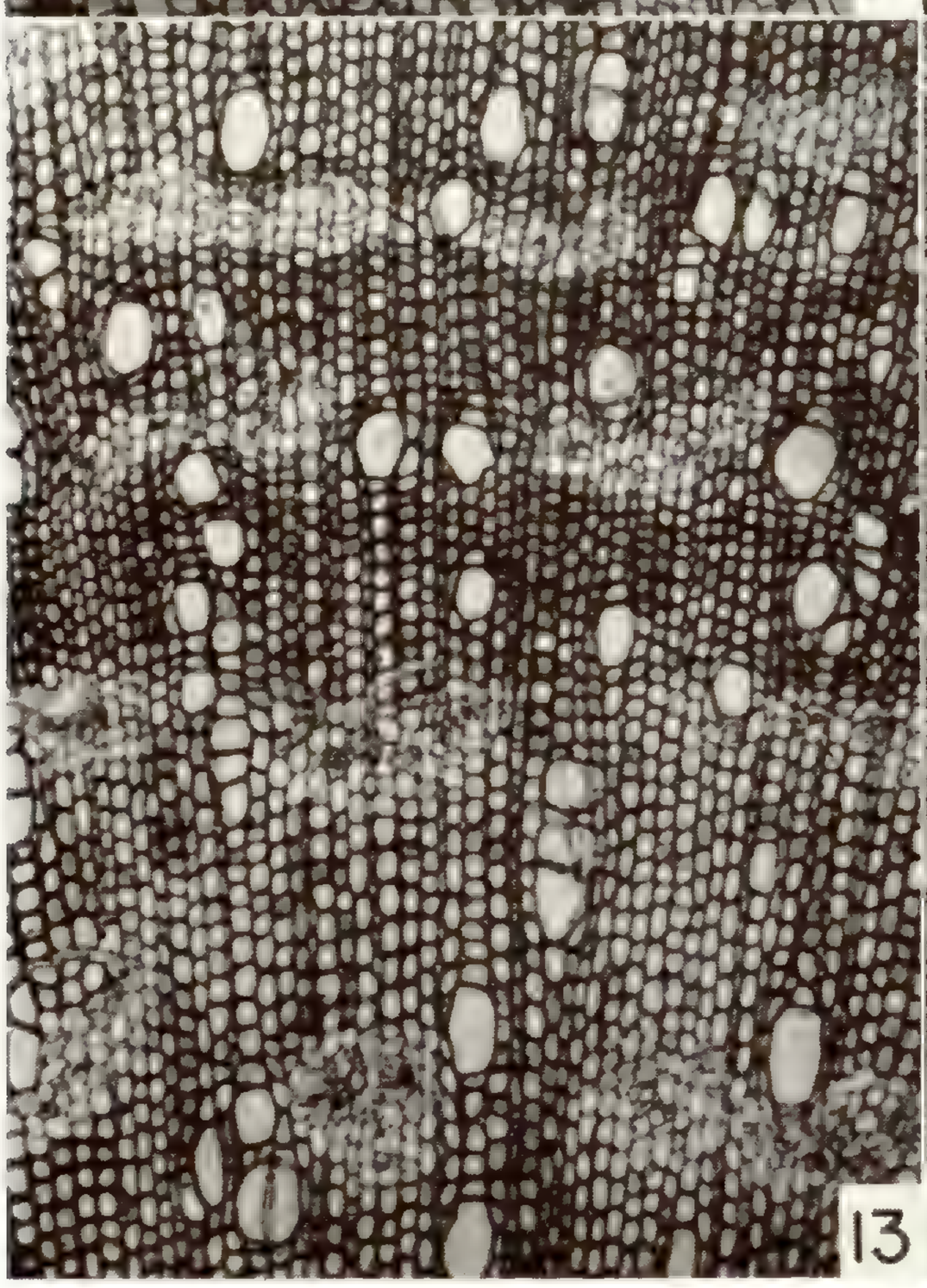
The physiological significance of vestured pits is not at all clear, and none of the literature cited above, or references discussed by those authors offers any speculation on this point. The diagnostic value of these pits in identification of woods, has, however, been stressed. To be sure, presence of vestured pits offers a very strong line of evidence linking Onagraceae to other myrtalean families: Punicaceae, Lythraceae, Crypteroniaceae, Sonneratiaceae, Combretaceae, Myrtaceae, and Melastomaceae. Because of the pervasive presence of this feature in Myrtales, as well as its presence in all but a few Onagraceae, one would assume that lack of vesturing in those few Onagraceae where it is absent or minimal represents a phylogenetic loss of warts within pit cavities. If, as appears likely from the literature, appearance of warts in vestured pits is ontogenetically a rather sudden event that occurs when lignification is complete, one can say that absence of vesturing in those Onagraceae without vesturing represents a foreshortening of the process of vessel-wall formation.

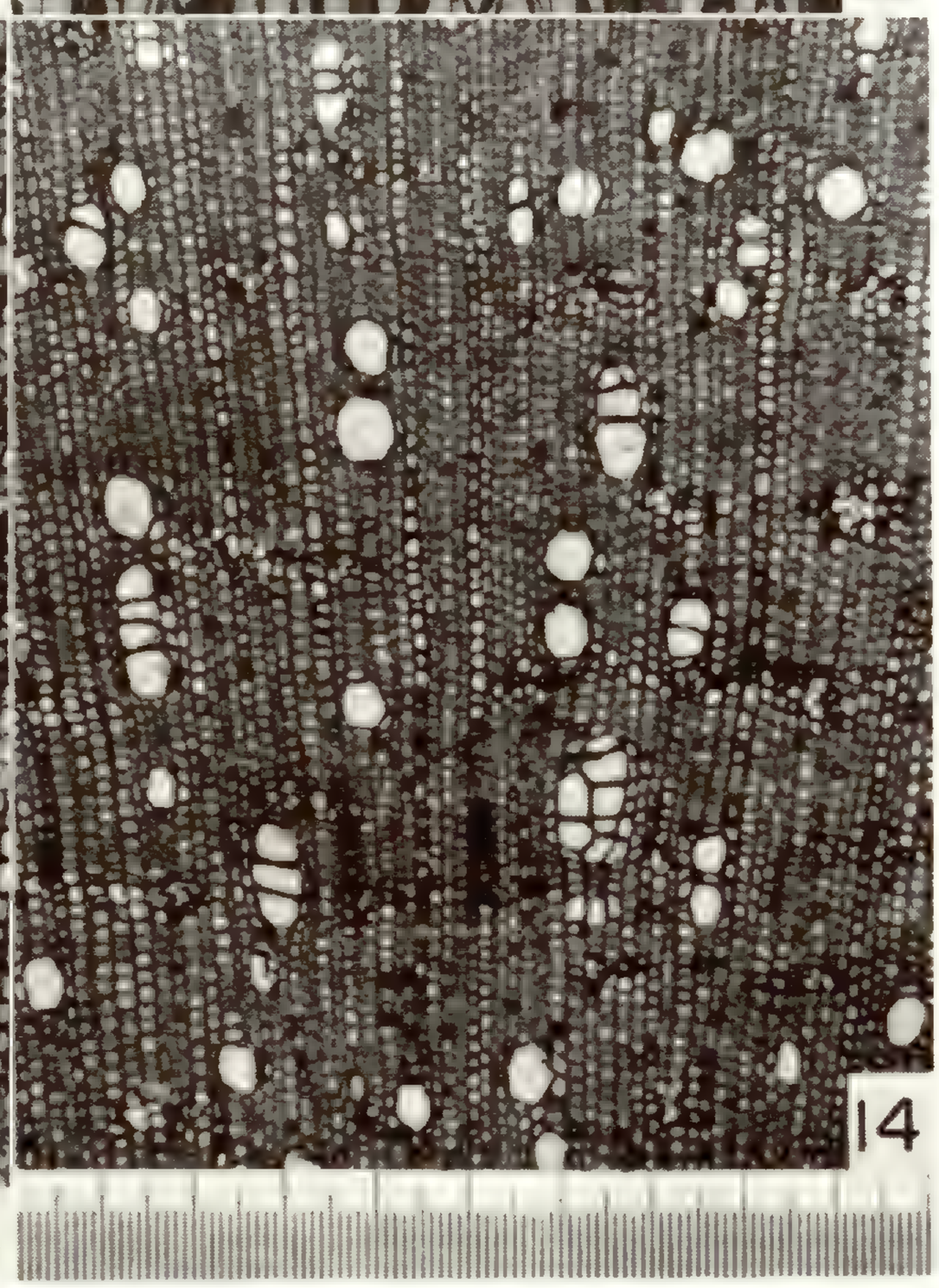
Pit Arrangement and Shape.—One can characterize pitting in all Onagraceae as alternate, although one unfamiliar with wood anatomy would perhaps, upon viewing wood sections, say that opposite and scalariform pitting is present on vessel walls. This seeming paradox, as correctly implied by Metcalfe & Chalk (1950), results from the fact that pits in many species are laterally widened, interrupting a clearly alternate pattern (see, for example, Figs. 52–53). One must stress that these patterns have nothing at all to do with opposite pits in vessels of primitive dicotyledons, where the opposite condition results from fragmentation of the long pits of a scalariform pattern. That the elongate pits are derived secondarily from circular alternate pitting patterns can be said to be prefigured by the occurrence, even in those species with circular pits (Fig. 51), by the presence of slit-like pit apertures.

Of Onagraceae in the present study, elongate pits are most abundantly represented in *Fuchsia fulgens*, *F. tuberosa*, *Lopezia grandiflora*, *L. langmaniae* (Fig. 52), *L. lopezioides* (Fig. 53), *L. longiflora*, *L. miniata* subsp. *miniata*, *L. miniata* subsp. *paniculata*, *Gaura sinuata*, and *Xylonagra arborea* subsp. *wigginsii*. Some of these could be said to have a pseudoscalariform pattern of pitting on lateral walls of vessels, in fact. Vessel–parenchyma pitting shows more prominently elongate and enlarged pits than does intervascular pitting, as can be seen from the scanning electron photomicrographs of Butterfield & Meylan (1973) for *Fuchsia excorticata*. Of Onagraceae in the present study in which I observed only circular or slightly oval pits as intervascular pitting, I could find elongate pits on vessel walls in contact with parenchyma: *Oenothera deltoides* subsp. *howellii*, *O. linifolia*, *Ludwigia octovalvis*, *L. uruguayensis*, *Zauschneria cana*, and *Hauya elegans* subsp. *cornuta*.

Pits markedly enlarged, as well as elongate, were observed in various Onagraceae. The list is much the same as for the Onagraceae that have elongate pits, but also includes a few herbaceous species with circular pits, such as *Oenothera deltoides* subsp. *howellii* (Fig. 56). Pits both elongate and enlarged have been interpreted as an indication of minimal mechanical strength of vessel walls (Carlquist, 1975). This interpretation appears to be justified in view of the







FIGURES 11–14. Wood sections of *Lopezia*.—11–12. *L. lopezioides, Breedlove 8052*.—11. Transection showing extensive parenchyma zones containing phloem strands.—12. Tangential section; taken with partially polarized light. Raphides are bright.—13. *L. lopezioides, Breedlove 7268*. Transection. Phloem-containing bands are relatively small.—14. *L. grandiflora*. Transection. Phloem strands very small. [Magnification for Figs. 11–14 indicated by a photograph of a stage micrometer, enlarged at the same magnification as the photographs, beneath Fig. 14. Finest divisions of this micrometer = 10 μ.]

Onagraceae and Lopezieae in which these pits occur. The least degree of pit enlargement and elongation in Onagraceae characterize the genera *Fuchsia* and *Hauya*. One would expect this, since these are the woodiest genera of the family.

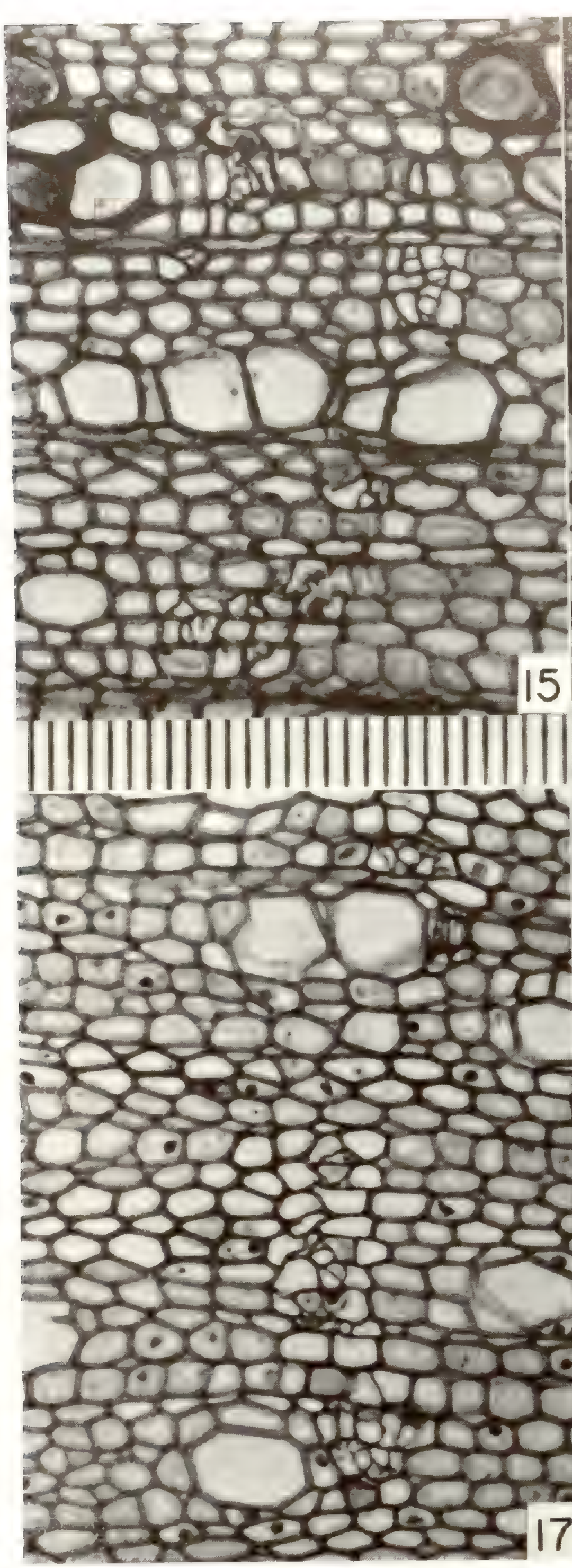
Grooves.—Pit apertures that are elongate, interconnecting with pit apertures of pits adjacent in a helix on a vessel wall were observed in *Lopezia longiflora* (Fig. 54). They were reported for *Gongylocarpus fruticulosis* subsp. *glaber* by Carlquist & Raven (1966).

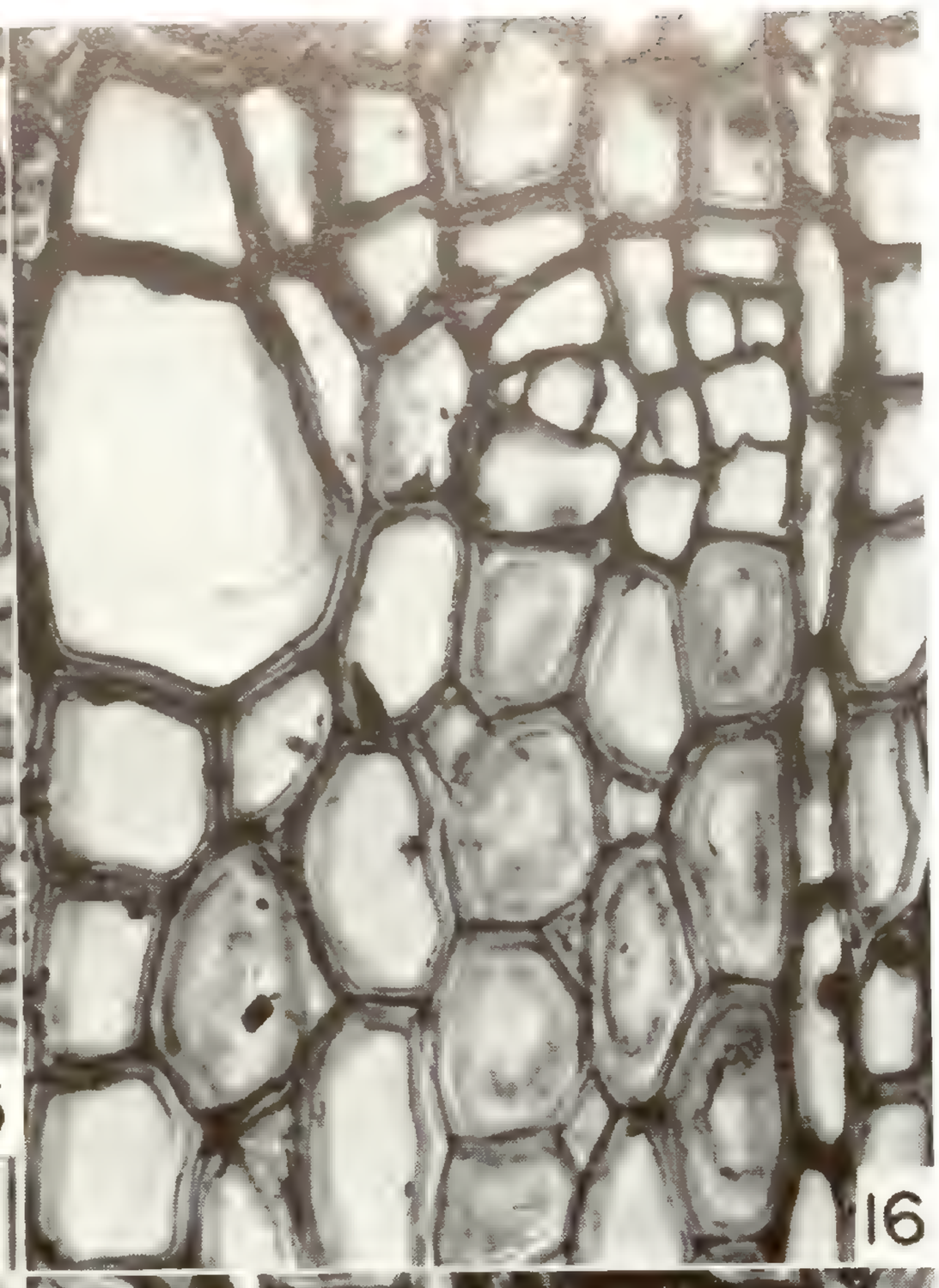
Perforation Plates.—Only simple perforation plates have been observed in secondary xylem of Onagraceae. That this expression is deep-seated is indicated by the fact that it occurs in primary xylem of Onagraceae studied by Bierhorst & Zamora (1965), with only occasional scalariform perforation plates in primary xylem. This is also true of *Lumnitzera littorea* Voist (Combretaceae), but simple perforation plates exclusively were observed by Bierhorst & Zamora (1965) in the myrtalean species *Leandra divaricata* Cogn. (Melastomaceae) and *Lumnitzera littorea* (Combretaceae). (The latter perhaps a second sample of that species, since it appears in two different listings on the basis of perforation plate morphology in the Bierhorst and Zamora paper.) More primitive primary xylem was reported by Bierhorst and Zamora for *Tristania* (Myrtaceae). This is interesting since the only myrtalean family in which scalariform perforation plates have been reported is Myrtaceae, and there only in a very few species (Metcalfe & Chalk, 1950).

The orientation of end walls of vessels in secondary xylem of Onagraceae could be said to be roughly transverse, but with considerable fluctuation. This fluctuation is based largely on the diameter of the vessel and the intrusiveness of the end wall on which the perforation plate is borne. Thus, the most nearly transverse perforations would be expected in the widest vessel elements—which also possess minimal intrusiveness of tips, in general. Examples of oblique end walls are not difficult to find, and can be seen, for example, in Figs. 24, 28, 32, and 36. Because of the correlation with vessel diameter just mentioned, I doubt that oblique end walls should be considered a relictual presence of a primitive characteristic.

Libriform Fibers

Nature of Wall.—Imperforate tracheary elements of Onagraceae consist wholly of libriform fibers. Pits are exclusively simple, with no vestiges of borders. In some species with exceptionally wide, parenchymatous libriform fibers, such as *Lopezia longiflora* (Fig. 21) and *Xylonagra arborea* subsp. *wigginsii*, pit apertures are rather wide, rather than very narrow and slit-like. In examining transections of wood of Onagraceae, one is struck by the almost universal presence of gelatinous walls on fibers. In any given section, not all fibers possess markedly gelatinous walls. Gelatinous fibers may occur in patches as seen in a transection, but more frequently in a ring of approximately uniform thickness that extends around the entire stem. In *Clarkia xantiana*, an annual, all libriform fibers have gelatinous walls. The mode of occurrence of gelatinous-walled libriform fibers in Onagraceae does not suggest occurrence of tension wood, despite the similarity in appearance. For example, a photograph of tension wood in *Populus tremuloides* Michx. presented by Côté & Day (1965) is virtually identical with my photograph of





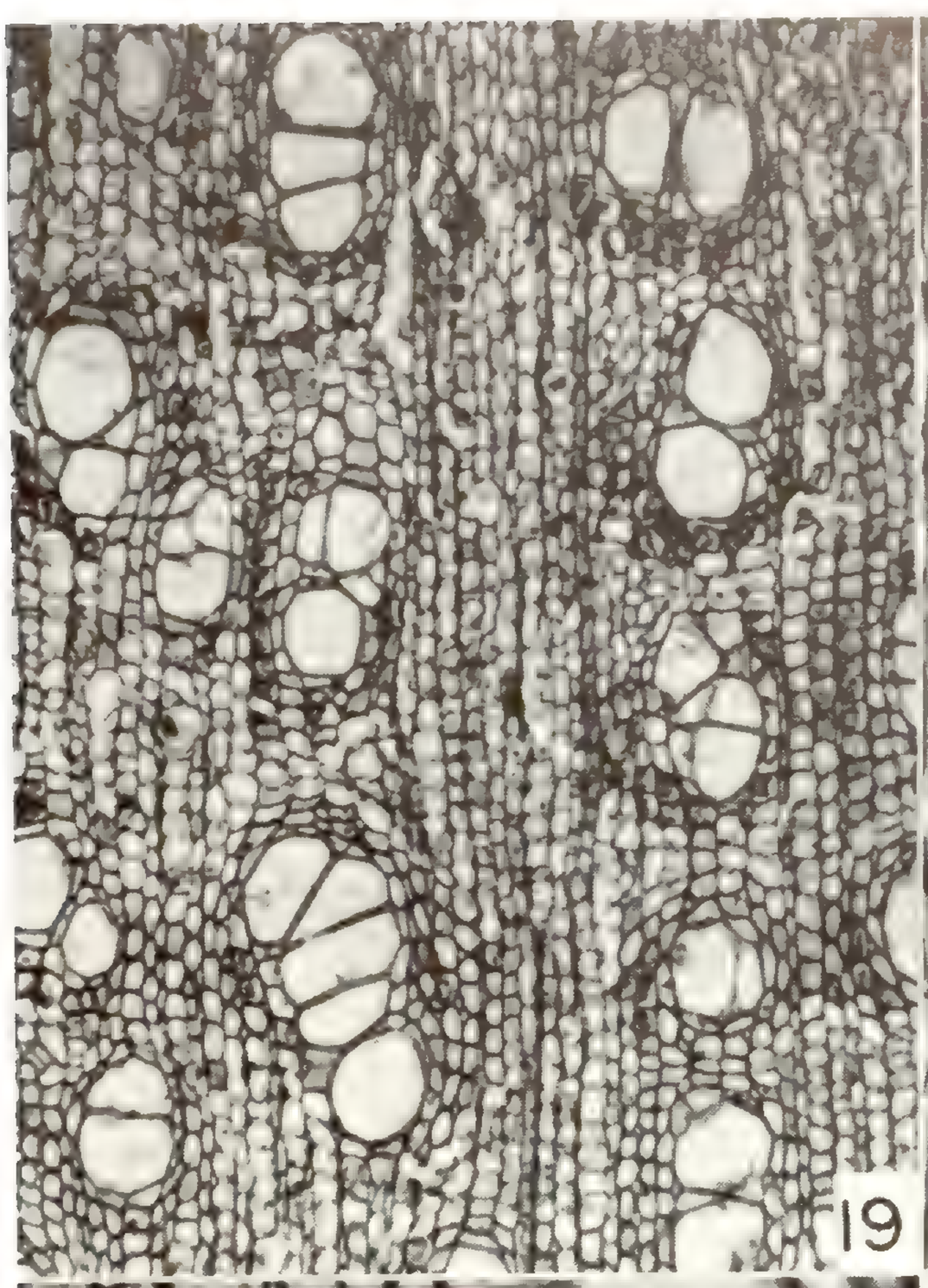
FIGURES 15–18. Wood transections of *Lopezia* to show nature of interxylary phloem and of gelatinous fibers.—15–16. *L. miniata* subsp. *miniata*.—15. Section (rays shown running from left to right) to show phloem.—16. View of vessel, phloem strand, and fibers.—17–18. *L. racemosa* subsp. *racemosa*.—17. Section (rays shown running from left to right) to show phloem strands.—18. View of vessel and gelatinous fibers. [Magnification scale for Figs. 15, 17 shown below Fig. 15; magnification scale for Figs. 16, 18 below Fig. 18. Each of these scales is a photograph of a stage micrometer enlarged at the same magnification as the photographs to which they pertain. The divisions of these scales = 10 μ.]

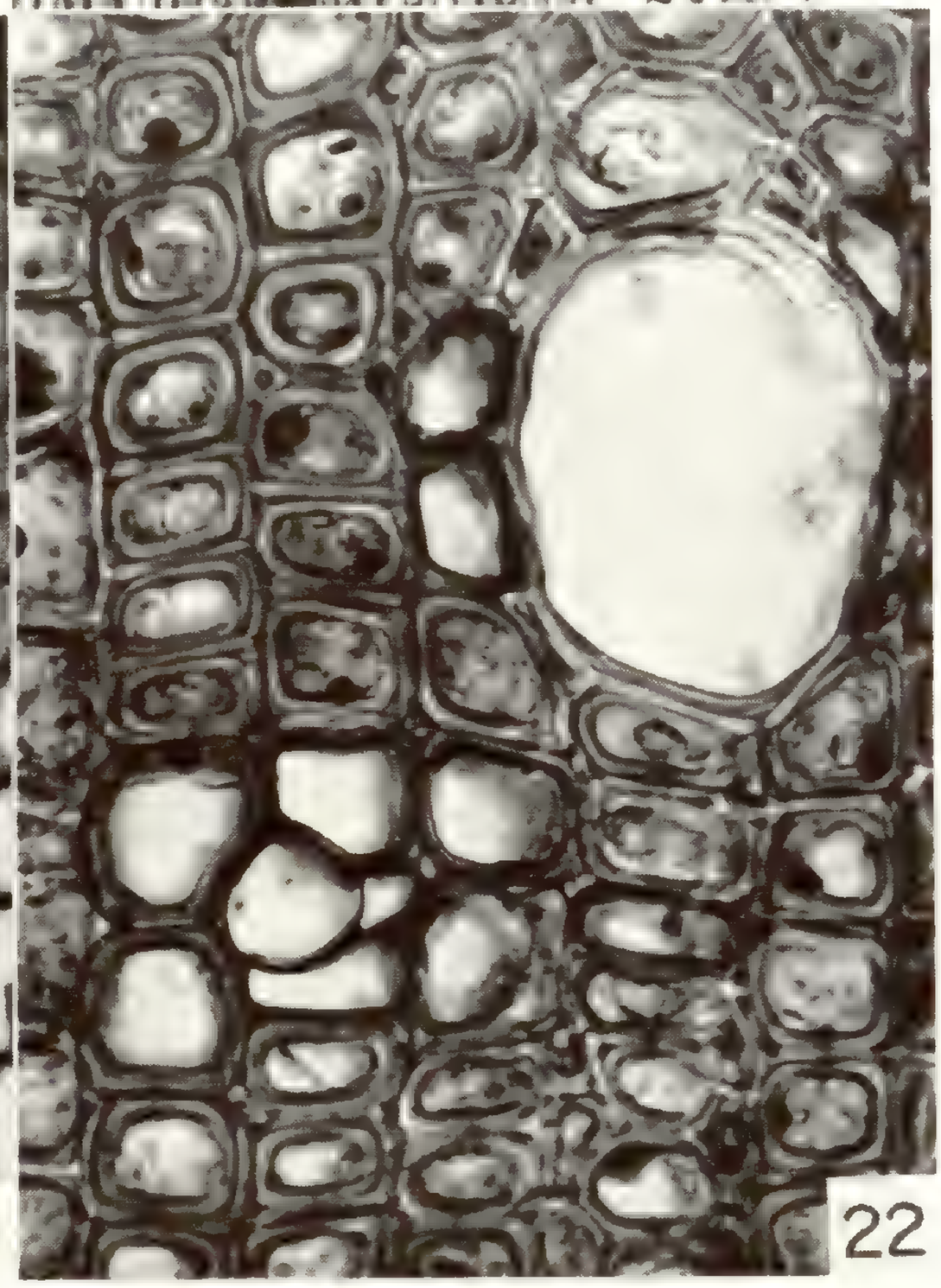
gelatinous fibers in *Xylonagra arborea* subsp. *wigginsii* (Fig. 33). However, mode of distribution within stems of Onagraceae and the fact that the majority of the family has relatively little wood speaks against the interpretation of gelatinous fibers as tension wood, although this cannot be ruled out for all species certainly.

In only a few species of Onagraceae were fibers with a non-lignified inner wall (the "G" layer of Côté & Day, 1965) not observed. Species with few or no gelatinous fibers include *Calylophus serrulatus*, *Camissonia megalantha*, *Lopezia lopezioides*, *L. miniata* subsp. *paniculata*, and *L. racemosa* subsp. *moelchenensis*. Gelatinous fibers may have a slightly differentiated inner wall, as in *Lopezia semeiandra* (Fig. 22). In most Onagraceae, the inner wall is thick, shrinks from the outer, lignified wall during fixation or preparation of slides, and may be displaced by sectioning (Figs. 25, 33). In a very few, the inner, non-lignified wall is very thick (Figs. 16, 18). In these latter species, the wall may have been expanded by the use of acetic acid in the fixative. In any case, in the fibers shown in Figs. 16 and 18, the inner wall is unusually thick.

Because the growth forms of most Onagraceae with gelatinous libriform fibers suggest no appreciable function of the fibers as tension wood, an alternative function might be sought, namely, water storage. To be sure, the inner gelatinous wall does show birefringence with polarized light, demonstrating presence of cellulose in most species. However, its non-lignified nature suggests a high degree hydration in the living condition. I note from monographs such as that of Plitmann, Raven & Breedlove (1973) and from my own field observations that many Onagraceae flower in the dry season. *Clarkia*, a vernal annual, flowers much later than do most vernal annuals. *Zauschneria* flowers at the end of the summer, before winter rains. Storage of water in highly hydrated gelatinous fibers may be correlated with this habit. Although a seemingly unlikely explanation, storage by a plant of water in gels formed by the cell wall is not unprecedented. The Madiinae (Asteraceae, tribe Heliantheae) have similar flowering habits, clearly correlated with storage of water in pectic gels extruded into intercellular spaces of leaves (Carlquist, 1957, 1959).

Fiber Septation and Nucleation.—As the column headed Libriform fibers in Table 1 indicates, very few Onagraceae were found to lack either septa or nuclei in libriform fibers. Absence in the two collections of *Hauya* may be based on the fact that dried wood samples were studied. Septate fibers normally have a single septum (Fig. 47). In *Ludwigia octovalvis*, two or three septa per fiber may be present. The presence of either septa or nuclei or both are indicative of longevity of protoplasts in libriform fibers. Presence of starch, mentioned in a later section, is an additional indication. In other words, libriform fibers of virtually all Onagraceae have some of the aspects of parenchyma: they may be considered libriform fibers functioning as parenchyma, in essence. Wolkinger (1970) notes four species of *Fuchsia* in his survey of living wood fibers. He also reports such fibers in the closely allied families Lythraceae (*Cuphea ignea* A. DC., *Lagerstroemia indica* L.) and Punicaceae (*Punica granatum* L.). Septate fibers photographed by means of scanning electron microscopy have been figured by Butterfield & Meylan (1973).





FIGURES 19–22. Wood sections of *Lopezia*.—19–21. *L. longiflora*.—19. Transection. Phloem-bearing parenchyma is abundant, libriform fibers few.—20. Tangential section. The few libriform fibers appear dark.—21. Transection. Strands of phloem below and at upper left; libriform fibers can be seen adjacent to vessel.—22. *L. semeiandra*. Transection showing starch-filled gelatinous fibers; phloem strand below left. [Magnification scale for Figs. 19–20 shown below Fig. 14; scale for Fig. 22 below Fig. 18.]

Libriform Fiber Lengths.—Average lengths parallel those of vessel elements closely, as can be seen in Table 1. The ratios for lengths of libriform fibers to those of vessel elements, also shown in Table 1, are perhaps lower than one would expect for a family of dicotyledons with specialized characteristics (see Carlquist, 1975). The ratios are, however, in accord with the predominantly herbaceous nature of the family. Were the family predominantly woody, one would expect that the ratio of libriform fiber lengths to those of vessel elements would exceed 2.0. Relatively long libriform fibers in a specialized family appear to connote greater mechanical strength. In Onagraceae, not only do relatively short libriform fibers suggest a moderate degree of mechanical strength, the thin-walled and gelatinous nature of the fibers, as well as the nature of vessel walls also connote low mechanical strength. In studying macerations of onagraceous wood, one can frequently see libriform fibers in which the broad body of the fiber bears constricted narrow tips. This appearance suggests a derivative of a fusiform cambial initial in which there has been relatively little apical intrusive growth.

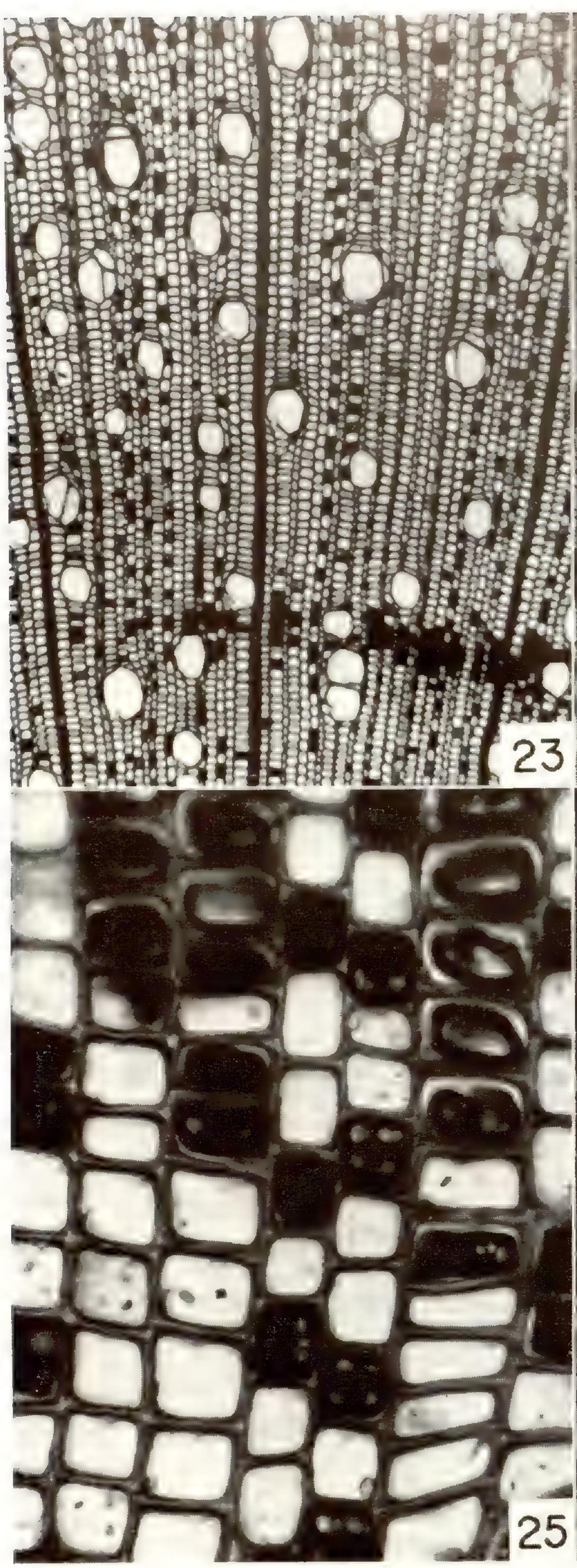
If mechanical strength is related to relatively long fibers, one would expect these in tree species. Libriform fibers averaging more than 700 μ in length were observed in *Fuchsia paniculata*, *F. parviflora*, and all collections of *Hauya*, validating this expectation. The large trunk of *Hauya elegans* subsp. *cornuta* (*Breedlove 10589*) not only had the longest libriform fibers in the family, it proved to have a notably high ratio between libriform fiber length and vessel element length. Also notably high in libriform fiber length are the species of *Ludwigia*. In this genus, which is not arborescent, longer tracheary elements may be related to very wet habitats, and long fibers may be a by-product of factors leading to occurrence of long vessel elements, for which a hypothesis is offered above.

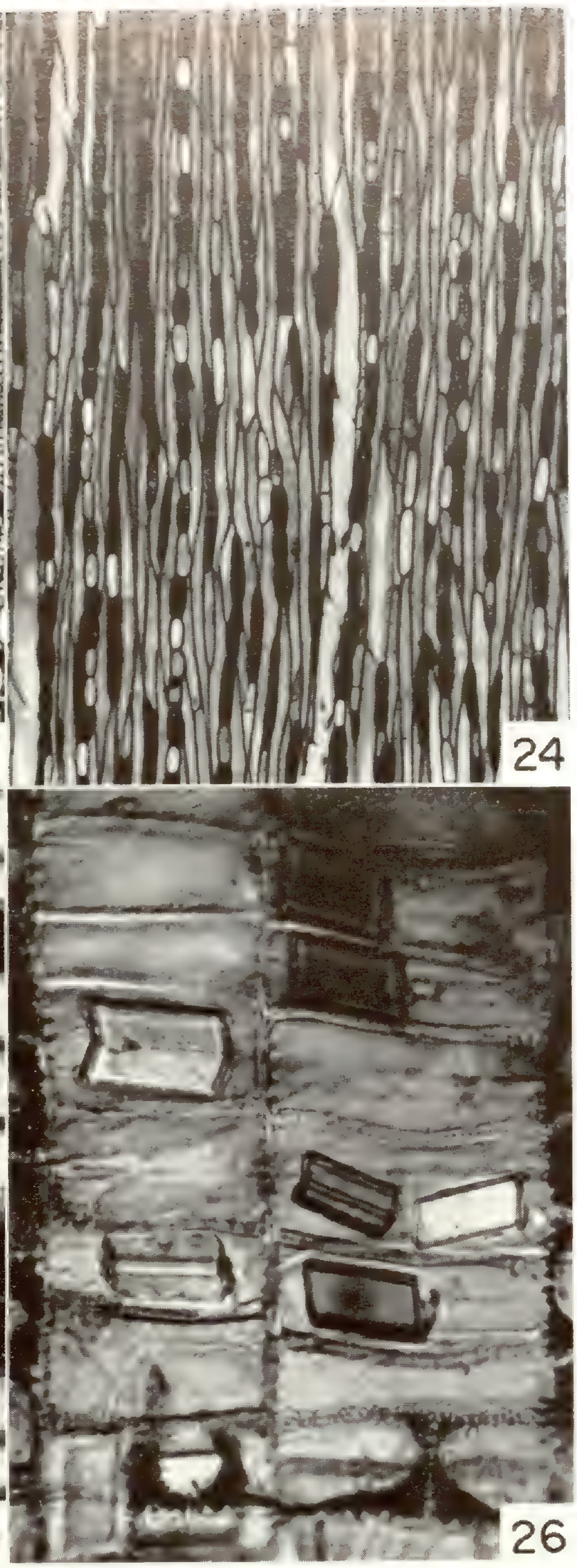
Wall Thickness.—Almost all Onagraceae could be said to have thin-walled fibers, if one disregards the thickness of gelatinous fibers. By "thin" I mean between 2 and 3 μ in thickness. Very thin-walled (1–2 μ) fibers were observed in *Calylophus hartwegii* subsp. *pubescens*, *Camissonia californica* (Fig. 27), *Fuchsia boliviana*, *Gaura villosa* subsp. *villosa* (Figs. 35, 39), *Heterogaura heterandra*, *Lopezia langmaniae*, *L. longiflora* (Fig. 19), *L. racemosa* (both subspecies), *Ludwigia octovalvis*, and *L. uruguayensis* (Fig. 23). Notably thick-walled (to 8 μ) fibers were observed in *Lopezia racemosa* subsp. *moelchenensis* and in *Gongylocarpus fruticulosus* subsp. *glaber*.

Fiber-like Cells in Interxylary Phloem.—Occasionally in species with interxylary phloem, one encounters in old phloem bands a few cells that appear to be thick-walled fibers. Such cells are illustrated here for *Oenothera linifolia* (Fig. 50). They apparently are derived from phloem parenchyma cells that develop thick walls and become lignified. Therefore, they should be considered sclereids rather than fibers.

Vascular Rays

Cell Shapes.—As the column headed Ray Histology in Table 1 shows, upright (erect) cells predominate in rays of most onagraceous woods. Only in the larger log of *Hauya elegans* subsp. *cornuta* (Figs. 8–10) are procumbent cells frequent. In the other Onagraceae, procumbent cells are infrequent. In some species,





FIGURES 23–26. Wood sections of *Ludwigia*.—23–25. *L. uruguayensis*.—23. Transection. Some ray cells and libriform fibers are filled with dark-staining deposits.—24. Tangential section. Rays are notably tall.—25. Transection. Starch grains, dark staining deposits visible; shrunken gelatinous walls in some fibers at top of photograph.—26. *L. octovalvis*, *Raven 6571*. Ray cells from radial section, showing prismatic crystals. Crystals are of various shades because they are variously colored under the partially polarized light used for this photograph. [Magnification scale for Figs. 23–24 shown below Fig. 14; scale for Figs. 25–26 below Fig. 18.]

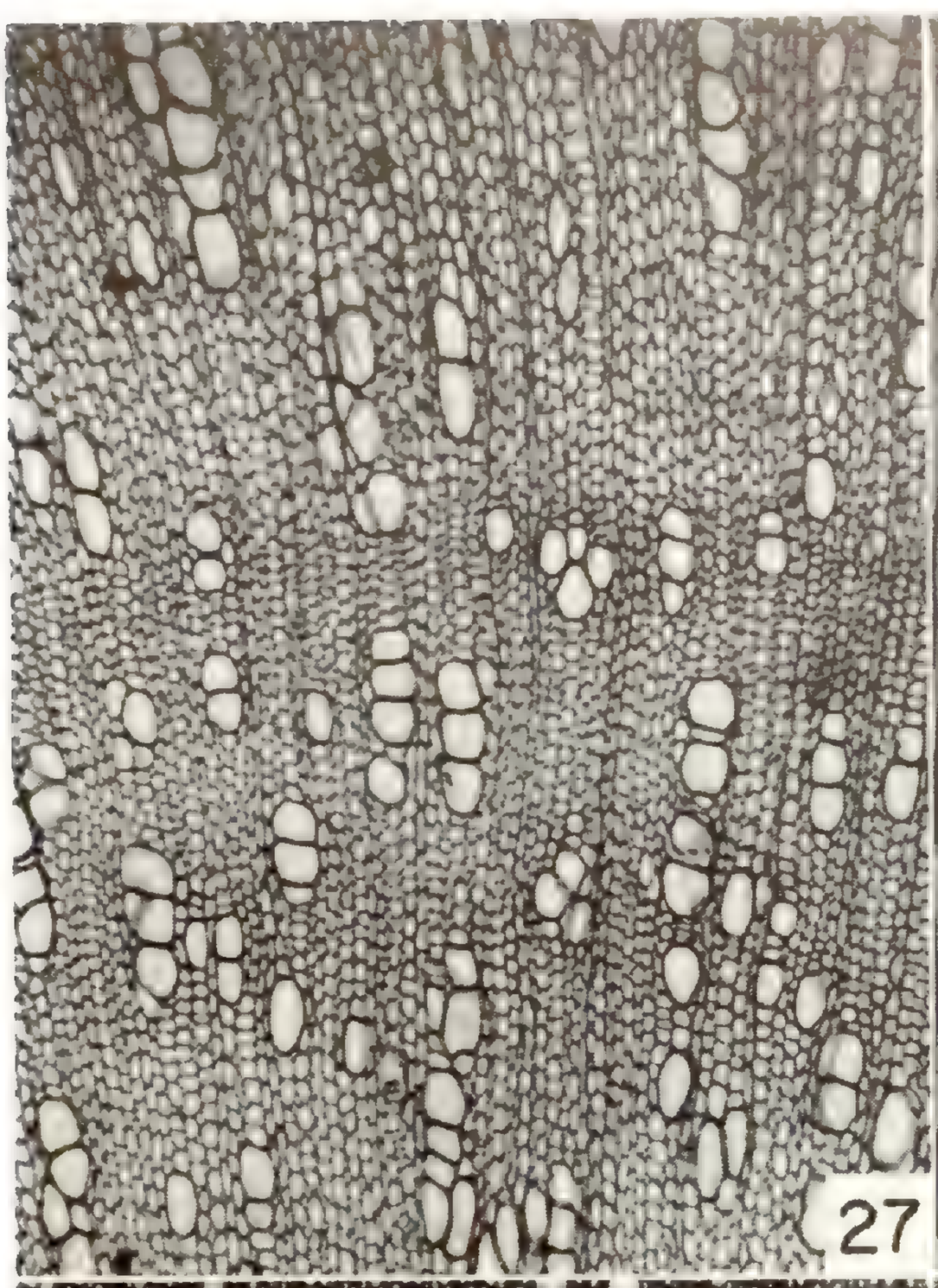
appearance of an occasional procumbent cell proves to be the result of a transverse division of an erect ray cell (*Gaura sinuata*). The predominance of erect ray cells might at first glance be thought unusual, considering the abundance of procumbent cells in rays of most families of woody dicotyledons. One is tempted to regard this tendency as an herbaceous mode of structure. However, one must take into account ray histology in the other myrtalean families. Erect to square ray cells exclusively are reported in Punicaceae and in Melastomaceae, subfamily Melastomoideae by Metcalfe & Chalk (1950), who also report uniseriate rays of this type in other myrtalean families but in combination with multiseriates containing procumbent cells.

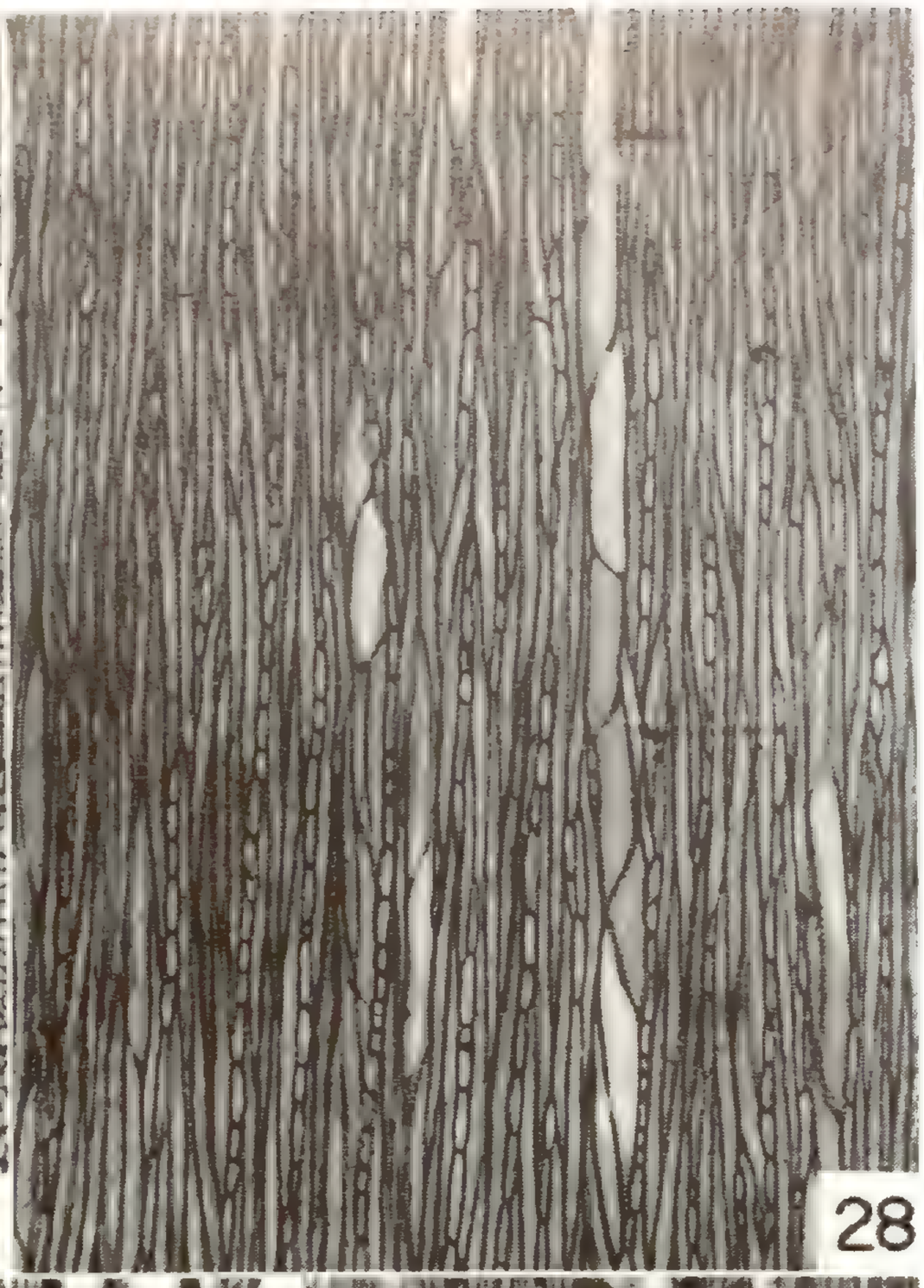
Comparison of stems of different ages in *Hauya elegans* subsp. *cornuta* shows that multiseriate rays broaden during growth of a tree (compare Fig. 8 with Fig. 10), and this broadening occurs by means of introduction of more numerous procumbent cells.

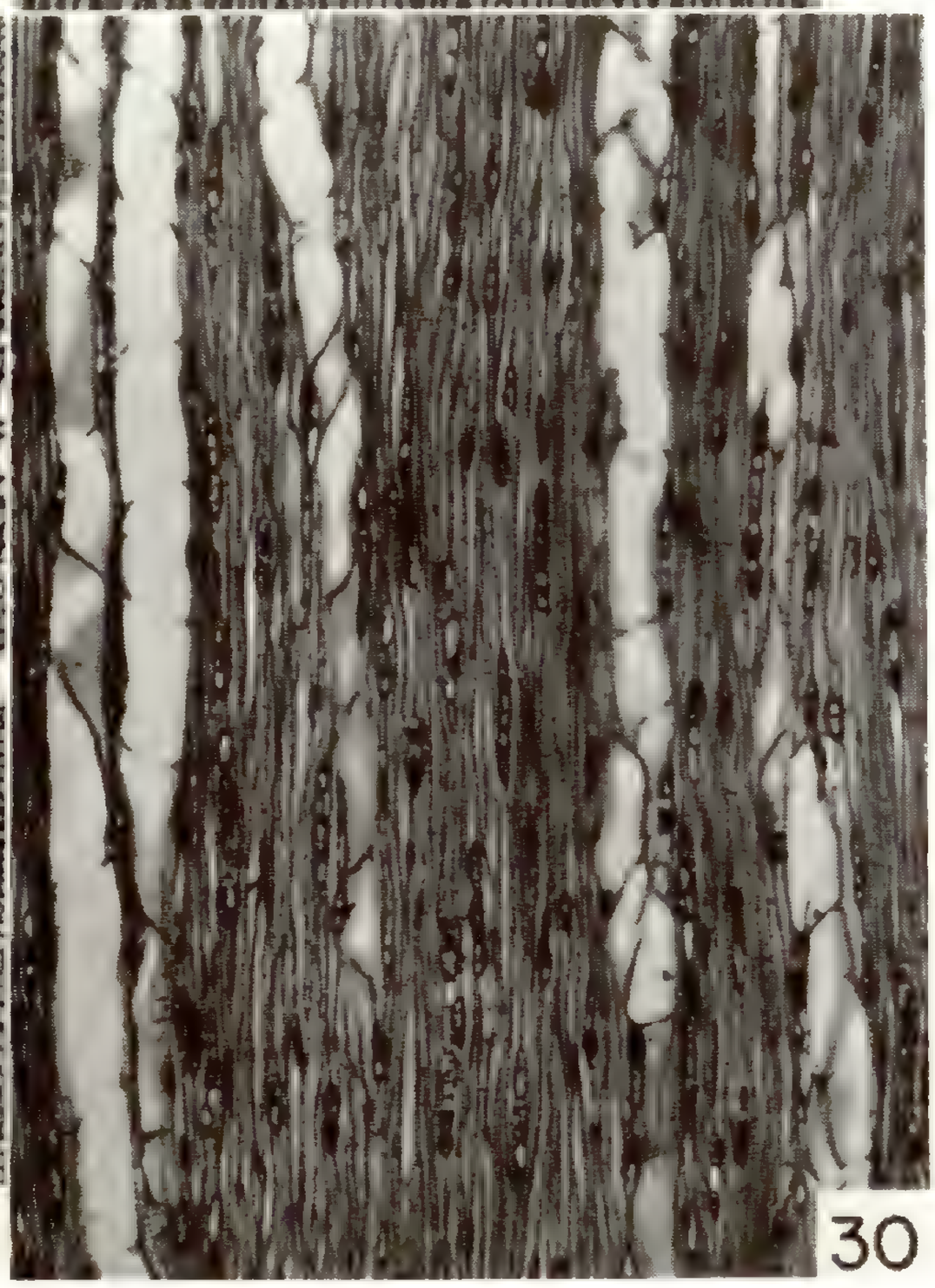
The predominance of erect ray cells in woods of Onagraceae, whether related to herbaceousness or not, may have the effect of compensating for paucity of axial parenchyma. One may note that where procumbent cells are most abundant (*Hauya*), so are axial parenchyma cells.

Ray Types.—Basically, most Onagraceae have multiseriate rays, with or without uniseriate wings; multiseriate rays are mostly little more than two cells wide, as indicated in Table 1 and Figs. 2, 8, 9, 12, 20, 24, 28, 32, and 36. Uniseriate rays are typically present also. The balance between multiseriates and uniseriates varies within the family. Uniseriates predominate over multiseriates in such species as *Fuchsia splendens*, *F. tuberosa*, *Lopezia lopezioides* (Fig. 20), *L. racemosa* subsp. *racemosa*, *L. riesenbachia*, *Calylophus hartwegii* subsp. *pubescens*, *C. serrulatus*, *Camissonia californica* (Fig. 28), *C. cheiranthifolia*, *Heterogaura heterandra*, *Oenothera deltoides* subsp. *howellii*, *O. linifolia* (Fig. 30), *Epilobium paniculatum*, and *Zauschneria cana*. Multiseriates are more numerous than uniseriates in most species of *Fuchsia* (*F. lycioides*: Fig. 2), both species of *Gongylocarpus* (Carlquist & Raven, 1966), *Xylonagra arborea* subsp. *wigginsii* (Fig. 32), *Ludwigia octovalvis*, and *Hauya elegans* subsp. *cornuta* (Figs. 8–10). These listings show a definite tendency, as suggested above, for increase in ray width with age and size of plant. Thus, most of the species in which uniseriates predominate over multiseriates are annuals or small shrubs, whereas the species in which multiseriates predominate are mostly medium to large shrubs or trees. Wide multiseriates have been reported by Metcalfe & Chalk (1950) for "*Fuchsia riccartonii*" (*F. magellanica* sens. lat.) and "*F. macrostemma*" (*F. magellanica* var. *macrostemma*). One can hypothesize that during growth, ray initials tend to subdivide, converting uniseriates into multiseriates and converting narrow multiseriates into wider multiseriates. This was observed in the case of *Calylophus hartwegii*, in which two growth rings were present in the sample studied.

Some Onagraceae have notably tall multiseriate rays: the genera *Fuchsia* (*F. lycioides*: Fig. 2) and *Ludwigia* (*L. uruguayensis*: Fig. 24) are notable in this regard. In these, multiseriates may narrow into uniseriate portions along their vertical length, as seen in a tangential section.







FIGURES 27–30. Wood sections of Onagreae.—27–28. *Camissonia californica*.—27. Transection. Libriform fibers are notably thin-walled.—28. Tangential section. Rays are predominantly uniseriate, tall.—29–30. *Oenothera linifolia*.—29. Transection from outer portion of xylem.—30. Tangential section. Rays are predominantly uniseriate, short. [All figures at magnification of scale shown below Fig. 14.]

Cell Walls.—Cell walls of rays tend to be of about the same thickness as libriform fibers in any given species. Where rays traverse bands of phloem-containing interxylary parenchyma, ray cell walls are non-lignified and thin (Figs. 12, 20). In the case of species in which ray cells have thick, lignified cell walls, pits among ray cells may be bordered. Pits are characteristically bordered in *Camissonia crassifolia* and *Hauya elegans* subsp. *cornuta*. Occurrence of bordered pits among ray cells is probably more common in dicotyledons than reports would indicate at present. However, Sastrapadja & Lamoureux (1969) have reported such pits in ray cells of a genus of Myrtaceae, *Metrosideros*.

Axial Parenchyma

Vasicentric Parenchyma.—As stated by Metcalfe & Chalk (1950), all Onagraceae can be said to have scanty vasicentric parenchyma, limited to a few cells around vessels. This condition is illustrated here most clearly for *Fuchsia tuberosa* (Fig. 49), in which transverse walls permitting identification of strands of parenchyma cells can be seen. The four cells of Fig. 45 are also vasicentric parenchyma cells. Although in some species of Onagraceae only a single strand of parenchyma cells may accompany a vessel, in none of the species studied were vasicentric parenchyma cells entirely lacking. Strands of vasicentric parenchyma are ordinarily three or four cells in length.

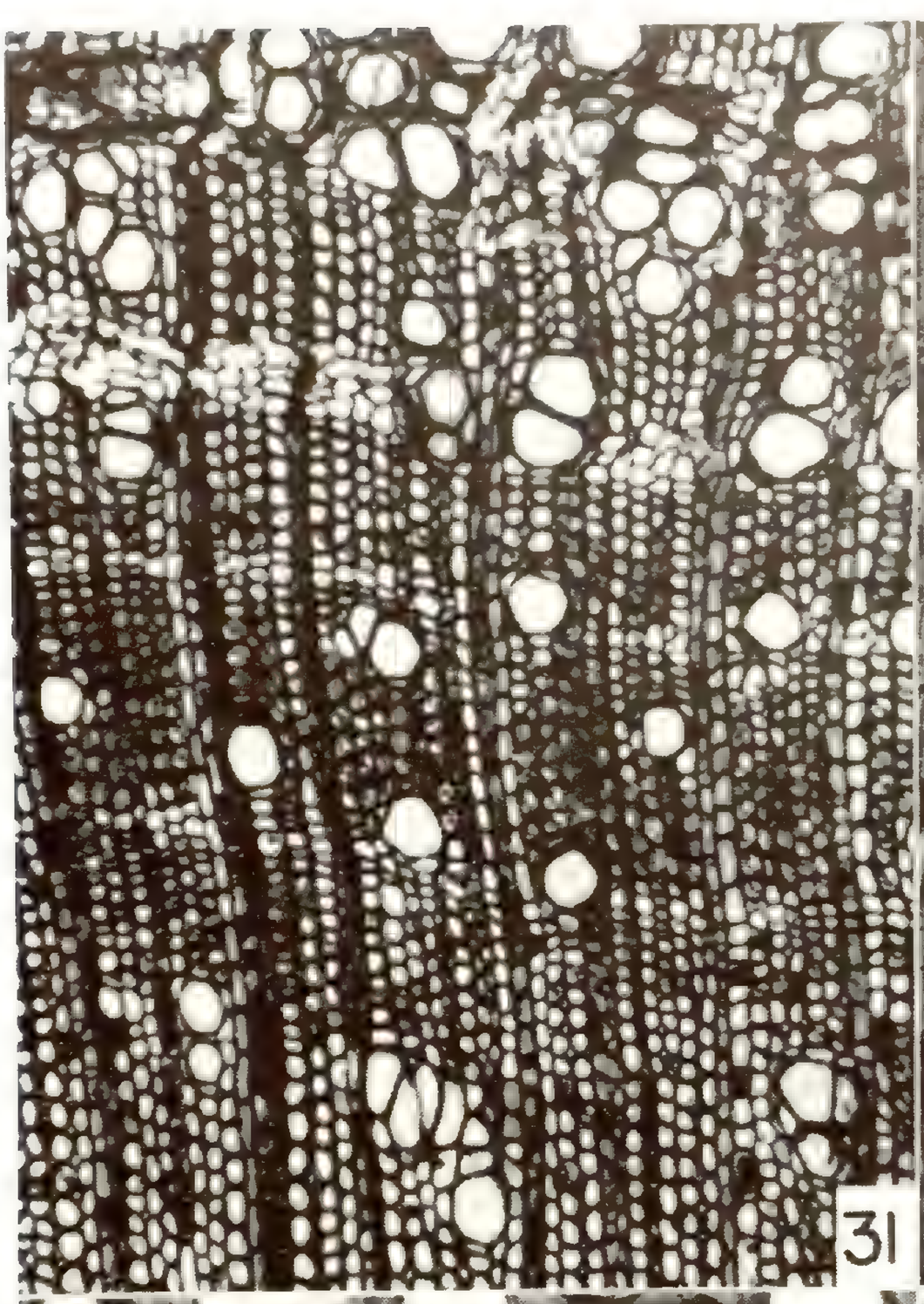
In *Hauya elegans* subsp. *cornuta* (Figs. 6–7) vasicentric parenchyma is relatively abundant, and completely sheathes vessels and vessel groups.

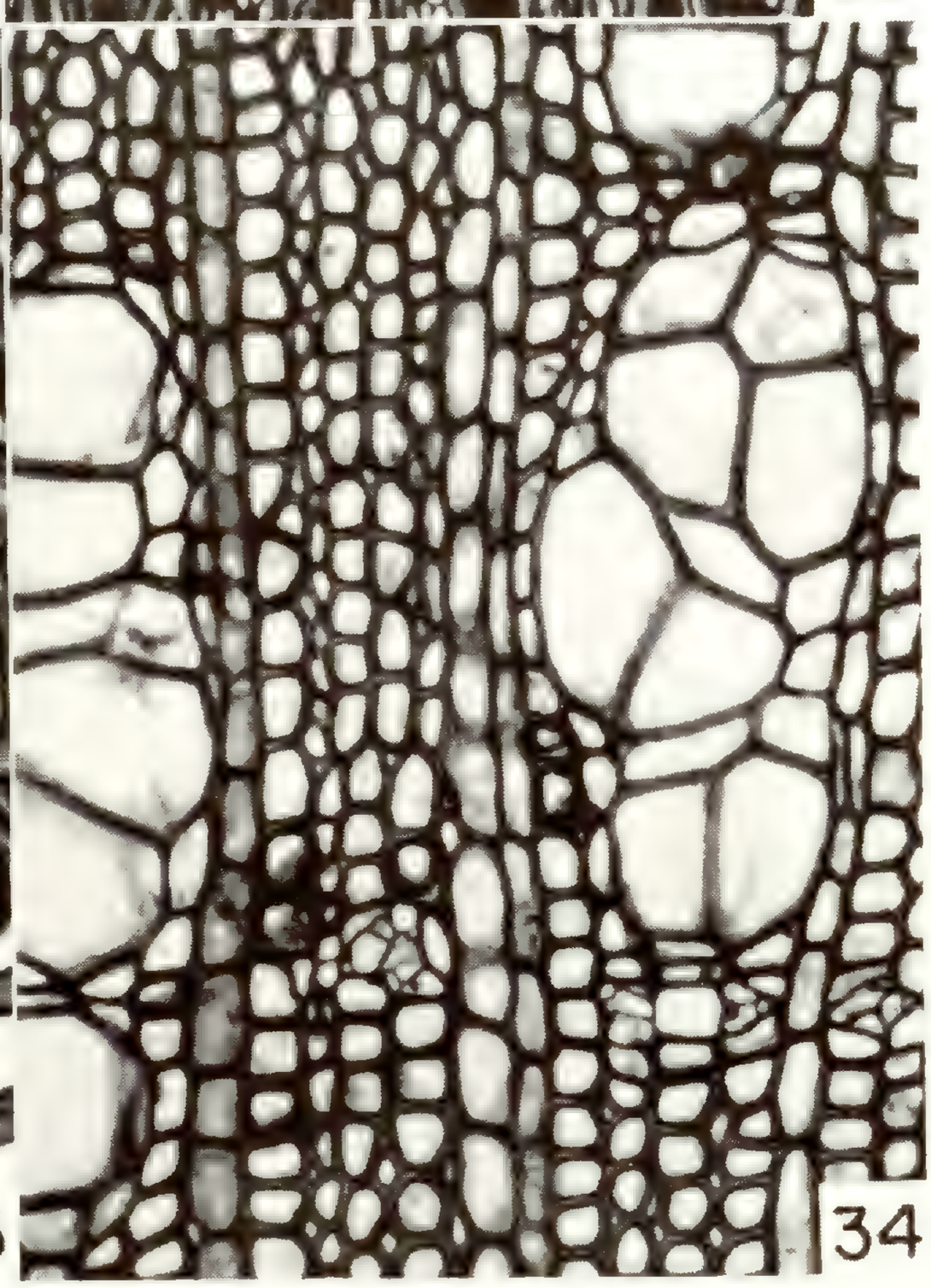
Apotracheal Parenchyma—Only in *Hauya elegans* subsp. *cornuta* (Figs. 6, 9) are there characteristically bands of apotracheal parenchyma that do not include phloem. There is no interxylary phloem in *Hauya*. The parenchyma in these bands is identical with vasicentric parenchyma, not only in number of cells per strand, but in the presence of lignified walls. In the parenchyma associated with phloem in those Onagraceae that have interxylary phloem, parenchyma is non-lignified and is usually not subdivided into strands, or is only once septate (see Figs. 12 and 44, for example). Bands of parenchyma comparable to those of *Hauya* occur in *Lagerstroemia* (Lythraceae) and certain Melastomaceae (Metcalfe & Chalk, 1950).

No species of *Fuchsia* studied has apotracheal parenchyma or interxylary phloem, except for a single instance seen in *F. tuberosa* (Fig. 49). In the stem studied, a few thin-walled parenchyma cells were observed at the stem periphery in fascicular areas of the xylem. In stems of various dicotyledons—usually herbaceous—one occasionally encounters thin-walled libriform parenchyma formed at intervals, in addition to characteristic axial parenchyma, as in *Hemizonia*. I suspect that this is the phenomenon exhibited in the stem of *F. tuberosa* studied. *Xylonagra arborea* subsp. *wigginsii* (Fig. 31) has parenchyma bands not all of which contain phloem, although most do.

Tyloses

As Table 1 indicates, tyloses were observed in approximately half of the species studied here. They evidently are quite characteristic of *Fuchsia*, and are illustrated





FIGURES 31–34. Wood sections of Onagreae.—31–33. *Xylonagra arborea* subsp. *wigginsii*. —31. Transection. Partially or wholly compressed parenchyma bands above.—32. Tangential section. Dark-staining deposits in some ray cells.—33. Portion of transection. Shrunken gelatinous walls visible in libriform fibers.—34. *Oenothera elata*. Transection. Phloem strands below. [Magnification scale for Figs. 31–32 shown below Fig. 14; scale for Fig. 33 below Fig. 18; scale for Fig. 34 below Fig. 15.]

here in *F. boliviana* (Fig. 51). The beginning stages in formation of tyloses were clearly observed in *Lopezia lopezioides* (Fig. 45). Such early stages can also be seen in *Fuchsia tuberosa* (Fig. 49). In Fig. 45, the vasicentric parenchyma cells are expanding into adjacent vessels through virtually all the available pits. In that species, vessel–parenchyma pits are wide, so that this behavior is not unexpected. Undoubtedly, samples of Onagraceae other than ones utilized would yield additional examples of tyloses. One would not expect them to be frequent in annual or biennial species, and in only one annual (*Oenothera deltoides* subsp. *howellii*) are they recorded here.

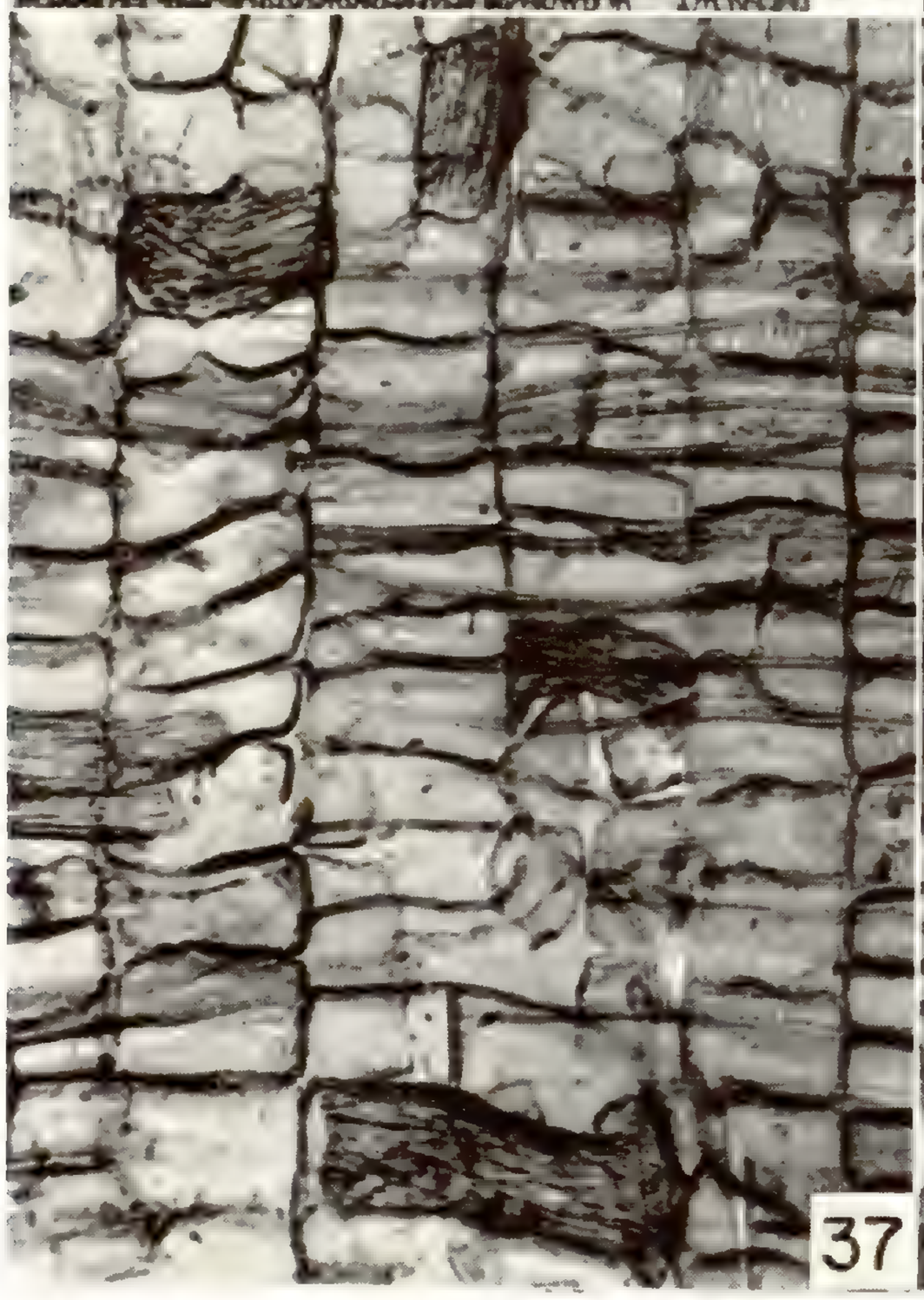
The occurrence of tyloses in Onagraceae seems linked to longevity of parenchyma cells. Liquid-preserved materials used in this study suggests that wood of Onagraceae is not mostly an accumulation of dead cells. Nuclei observed in ray cells, axial parenchyma cells, and libriform fibers prove the viability of these cells over a period of years. *Hauya* appears to lack tyloses. Perhaps parenchyma cells are more short-lived in this genus.

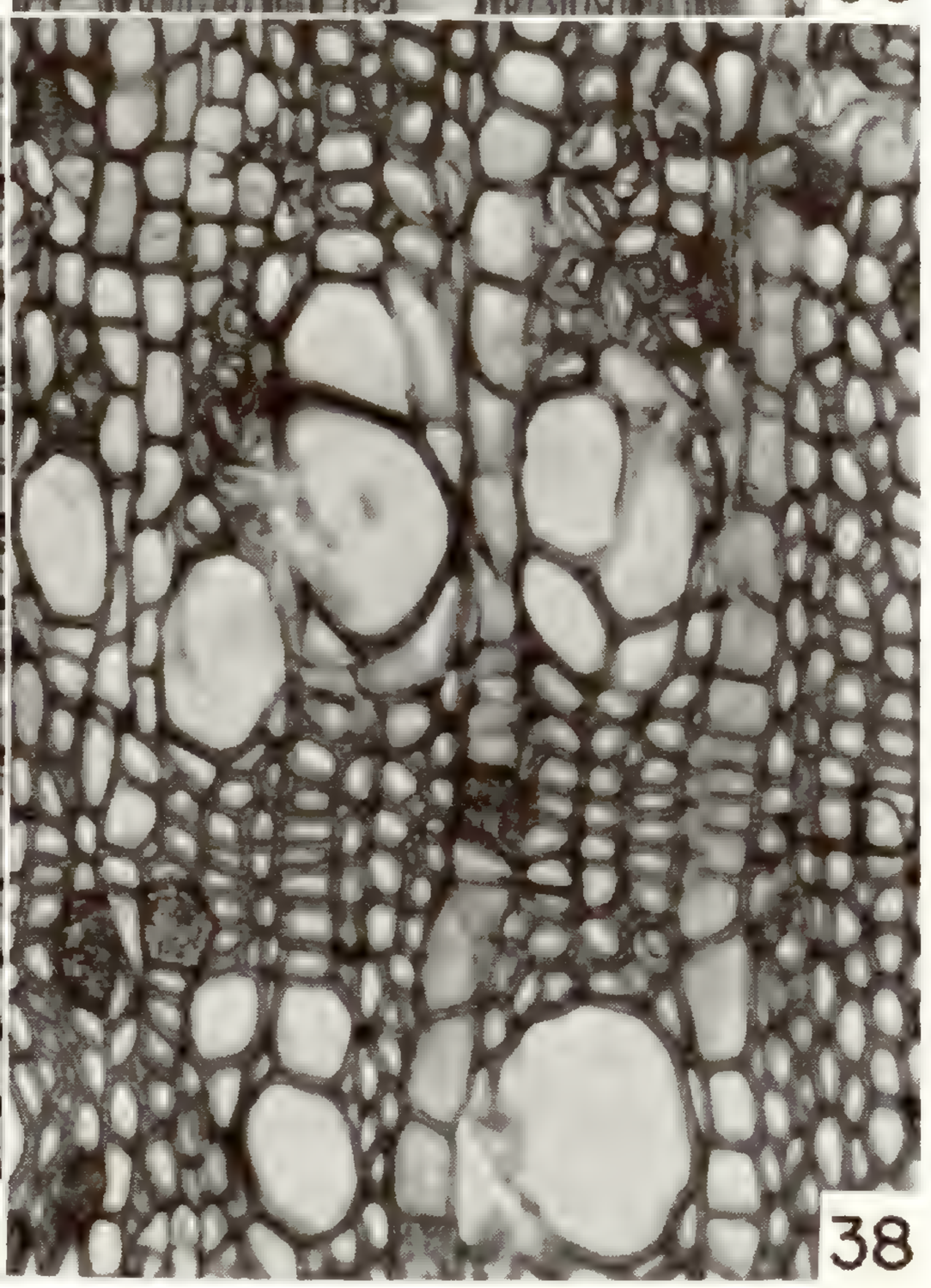
Tyloses have been reported for several genera of Lythraceae (Metcalfe & Chalk, 1950).

Interxylary Phloem

Myrtalean families apparently all have intraxylary phloem, which is not to be confused with interxylary phloem. Intraxylary phloem refers to strands of phloem between pith and primary xylem, whereas interxylary phloem (the "foraminate" type of Metcalfe & Chalk, 1950) consists of strands of phloem derived from a cambium on its internal face and thereby laid down within the secondary xylem. Cambial activity is "normal" in Onagraceae in the sense that only a single cambium, rather than successive cambia, is present. Although intraxylary phloem is characteristic of all myrtalean families (see Metcalfe & Chalk, 1950: 1343), not all myrtalean families have interxylary phloem. In addition to Onagraceae, interxylary phloem occurs in wood of Combretaceae (*Calycopteris*, *Guiera*, *Thiloa*, and African species of *Combretum*; Solereder, 1908; Metcalfe & Chalk, 1950); Melastomaceae (genera of Astronoideae and Memecyleae: Metcalfe & Chalk, 1950); and Lythraceae (*Lythrum salicaria* L., root only: Gin, 1909). Thus, interxylary phloem is absent from families probably very close to Onagraceae: Lythraceae (except as noted), Sonneratiaceae, Punicaceae, and Crypteroniaceae, as well as more distant families, such as Myrtaceae, Oliniaceae, and Penaeaceae.

As can be seen from Table 1, interxylary phloem is absent from the woody genera *Fuchsia*, *Hauya*, and *Ludwigia*. In Lopezieae, interxylary phloem was seen in all species studied except the shortlived annual *Lopezia riesenbachia*. The Onagreae in which interxylary phloem is absent are all annuals. Of the two Epilobieae studied, it is absent in the annual, *Epilobium paniculatum*, but present in the perennial, *Zauschneria cana*. Thus, both the most woody and the least woody species of Onagraceae tend to lack interxylary phloem. In the least woody species, one may hypothesize that the occurrence of secondary phloem and intraxylary phloem (still functional after onset of secondary growth) functionally suffice, and there is little selective value for inclusion of phloem strands within a xylem cylinder of relatively finite size.





FIGURES 35–38. Wood sections of *Gaura villosa* subsp. *villosa*.—35. Transection. Bands of phloem-containing parenchyma can be seen.—36. Tangential section. Uniseriate and multiseriate rays are about equally abundant.—37. Ray cells from radial section; some of the cells contain coarse raphides.—38. Portion of transection. Occurrence of raphides in some of the ray cells and fascicular parenchyma cells can be seen. [Magnification scale for Figs. 35–36 shown below Fig. 14; scale for Figs. 37–38 below Fig. 15.]

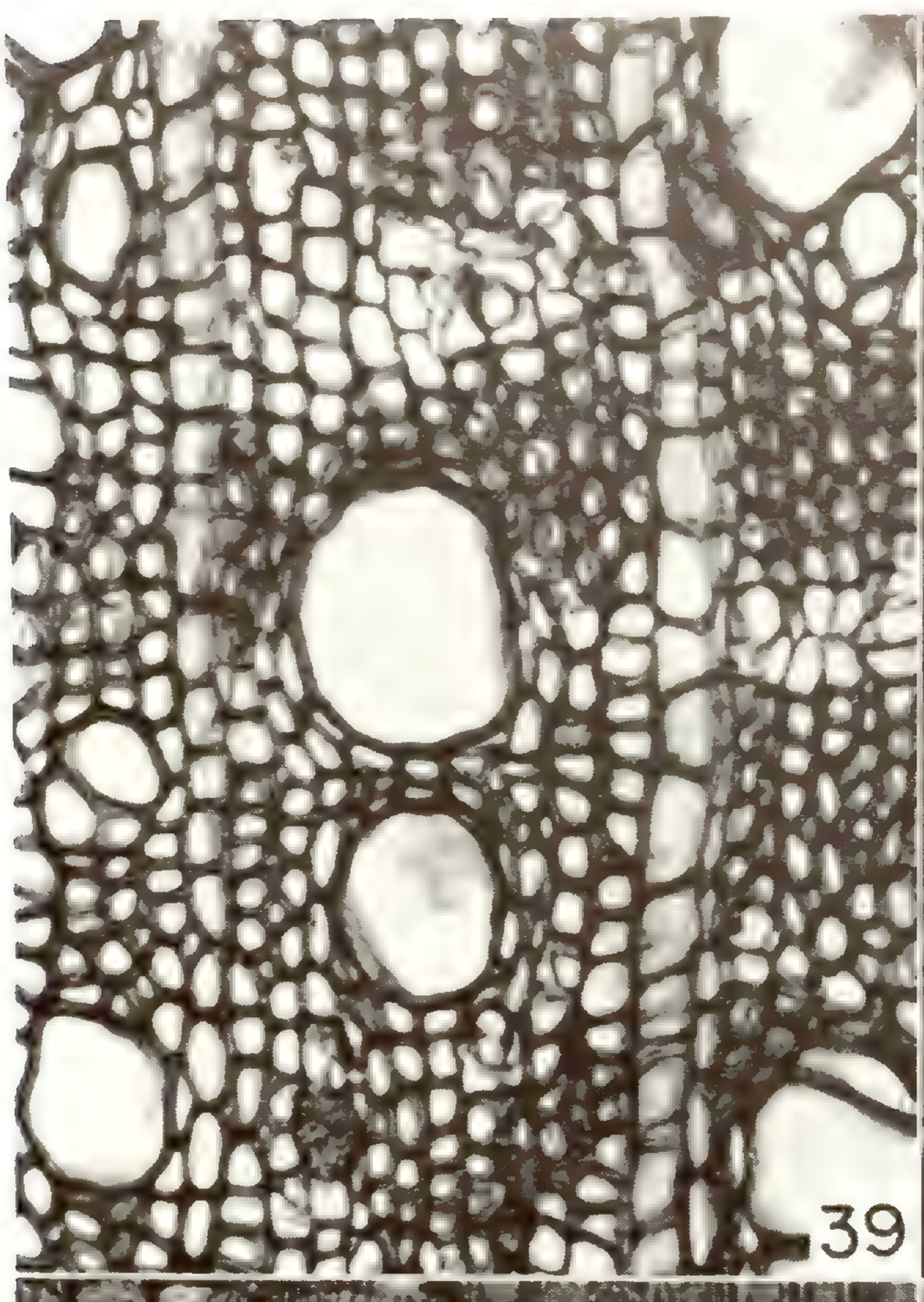
In the Onagraceae in which interxylary phloem strands occur, these take a wide variety of forms. The most striking of these would have not come to light except for the availability of wood samples of rather restricted species of *Lopezia*. In *L. lopezioides*, *Breedlove 8052* (Figs. 11–12; see also Figs. 43–44) wide bands and strands of phloem-containing parenchyma are present, although in the specimen *Breedlove 7268* (Fig. 13), the bands and strands are smaller. In *L. longiflora* (Figs. 19–21), the bands of phloem-containing parenchyma are so extensive that, in fact, they become the continuous phase of the fascicular xylem, with vessels and associated libriform fibers the discontinuous phase, dispersed as strands within the phloem-containing parenchyma. The phrase "phloem-containing parenchyma" has been used here deliberately because in the bands of parenchyma, phloem cells are localized rather than comprising the totality of the bands. In this respect, it is like the interxylary phloem illustrated by Singh (1944) for *Salvadora persica* L. As Figure 21 shows, sieve-tube elements and companion cells are separated from each other by numerous parenchyma cells. These parenchyma cells, to be sure, are non-lignified and identical to those in direct contact with sieve-tube elements and companion cells, so that all parenchyma cells of the bands and strands might be termed phloem parenchyma, provided that one keeps the above considerations in mind.

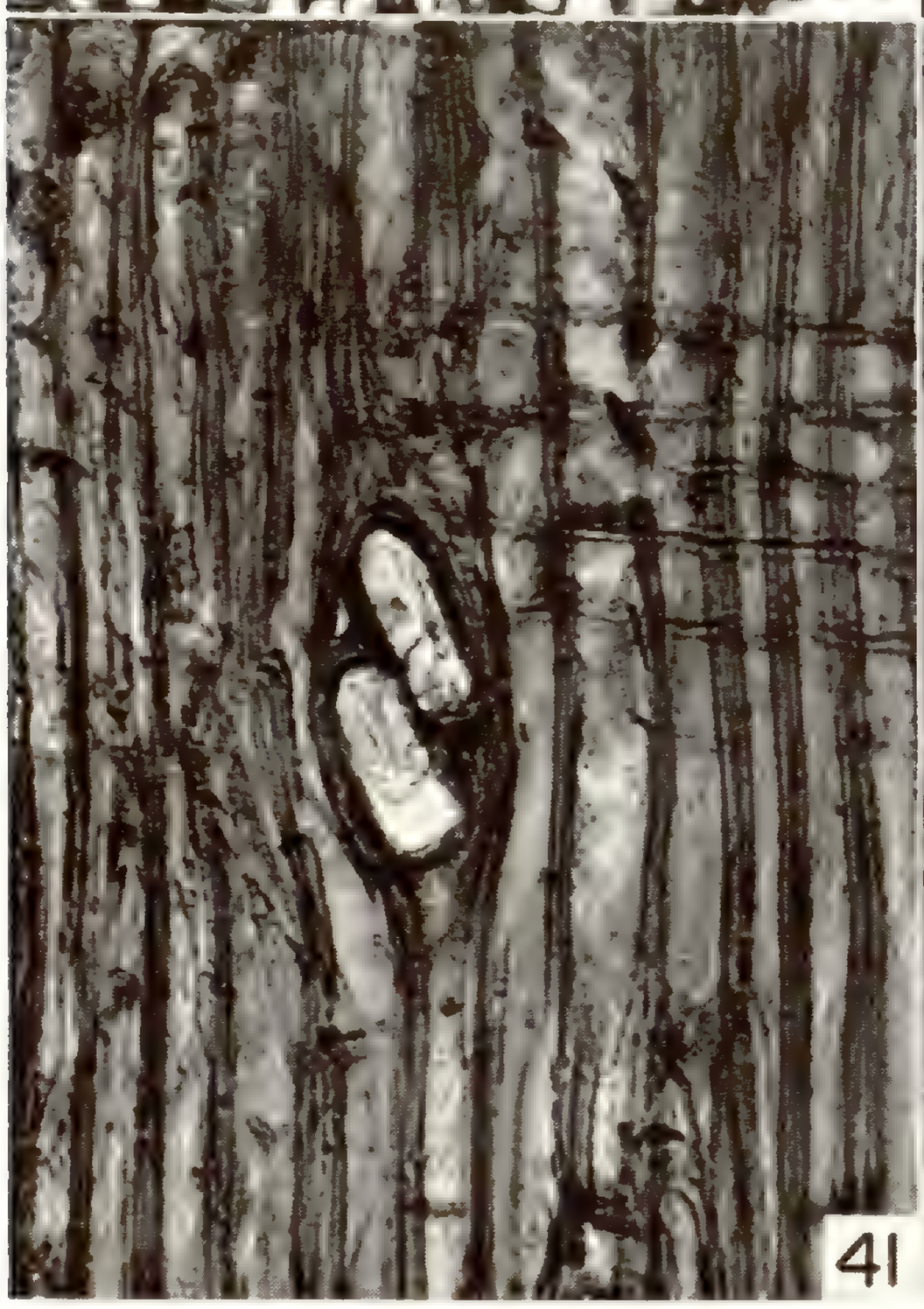
In other Lopezieae, the strands or bands of interxylary phloem are not expanded by large quantities of parenchyma, and the proportion of parenchyma to sieve-tube elements and companion cells is approximately what one would expect in ordinary secondary phloem. Such interxylary phloem is illustrated here for *Lopezia miniata* subsp. *miniata* (Figs. 15–16), *L. racemosa* subsp. *racemosa* (Fig. 17), and *L. semeiandra* (Fig. 22). Interxylary phloem strands of this type can be said to characterize the remaining Onagraceae in which interxylary phloem was observed, with the exception of *Xylonagra arborea* subsp. *wigginsii* (Fig. 31), *Camissonia crassifolia* and *Oenothera drummondii*. In the other species of *Oenothera*, as in *O. elata* (Fig. 34), phloem contains a minimum of parenchyma. In *O. linifolia*, a single growth ring, beginning with a band of phloem-containing parenchyma, was observed in the secondary xylem. Species of *Gaura* (Figs. 35, 39) tend to have a little more than the minimal amount of parenchyma, but not as much as in *Lopezia lopezioides*.

Sieve-tube elements of interxylary phloem in Onagraceae have transverse simple sieve plates. Both they and companion cells are the same length as cells of phloem parenchyma in a given species, and thus approximately the same length as fusiform cambial initials. Phloem parenchyma cells are occasionally subdivided into strands of two cells. Further details concerning contents of phloem parenchyma cells are given below.

Starch

One of the striking features of many onagraceous woods is the large quantity of starch present. Some parenchyma cells and fibers (Figs. 43, 46–48) seem to contain as much as any storage parenchyma cell in a tuber. Table 1 indicates the occurrence of starch I observed in Onagraceae. The reports of Table 1 must be considered minimal, and species for which starch is not reported here may well,





FIGURES 39–42. Wood sections of *Gaura* and *Hauya*.—39. *Gaura villosa* subsp. *villosa*. Transection. Phloem-containing parenchyma above and at right, middle. Shrunken inner gelatinous walls visible.—40. *Gaura sinuata*. Radial section, showing prismatic crystals in fibers above and below ray; ray cells have dark-staining deposits; raphides (out of focus) form striate pattern, below right.—41–42. *Hauya elegans* subsp. *cornuta*.—41. Radial section, showing pair of encapsulated ("chambered") prismatic crystals in fibriform cell.—42. Radial section, showing close view of encapsulated prismatic crystal. [Magnification scale for Figs. 39–41 shown below Fig. 15; scale for Fig. 42 below Fig. 18.]

if collected in other seasons and localities, have starch accumulation. Butterfield & Meylan (1973) have presented scanning electron photomicrographs of starch grains in libriform fibers of *Fuchsia excorticata.*

Note should be taken of the differential sites of starch accumulation. Where parenchyma of the phloem-containing bands is abundant, starch tends to be stored there (Figs. 12, 43–44, 46–47). Where parenchyma in interxylary phloem strands is minimal, libriform fibers and ray cells tend to contain the starch (Figs. 25, 29, 48). In those species with no interxylary phloem, libriform fibers and rays serve for starch storage. Starch accumulation appears to be more abundant in species that have interxylary phloem, in general.

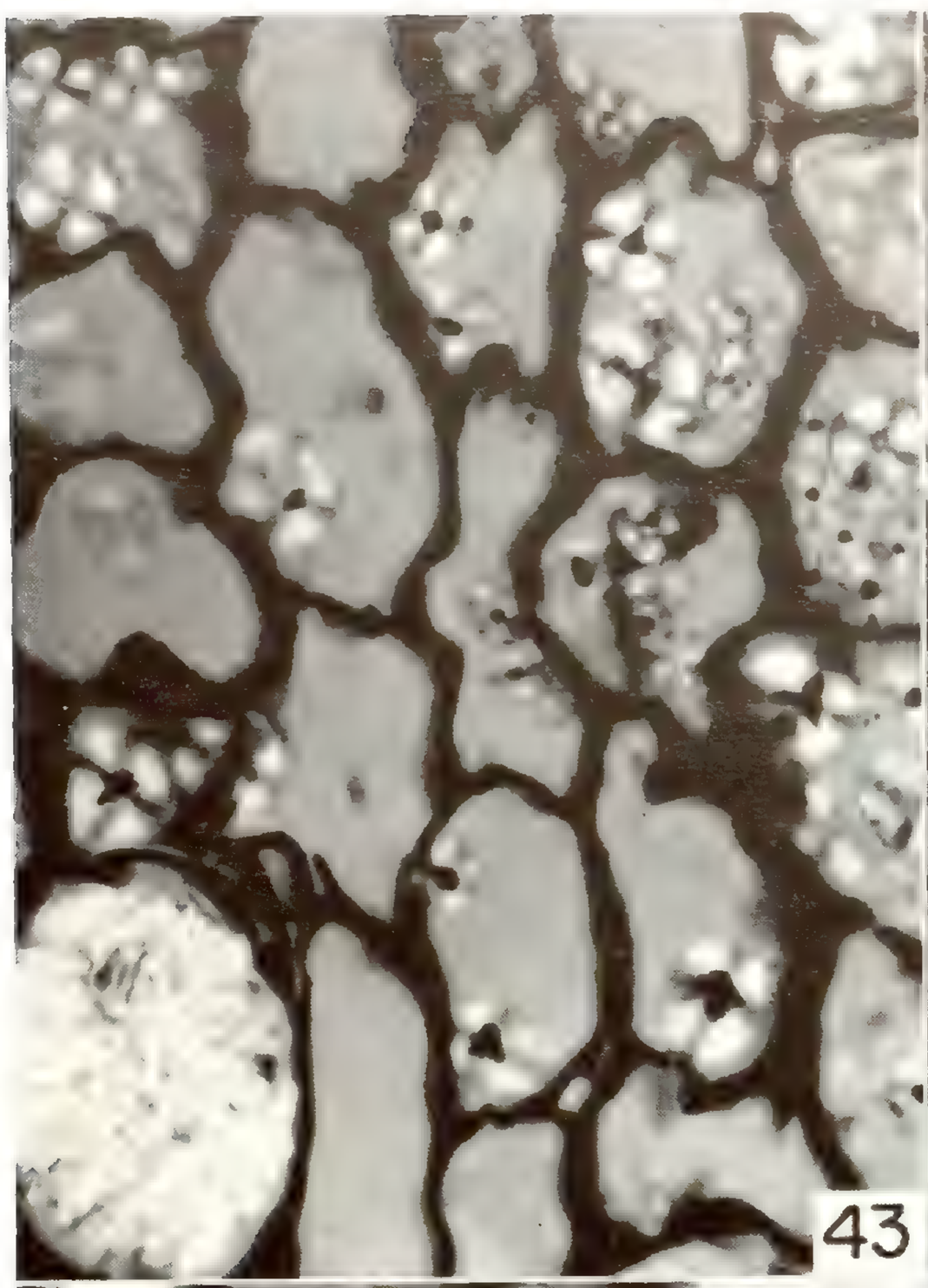
Crystals

Raphides.—Onagraceae are distinctive among myrtalean families in that all families of this order except Onagraceae lack raphides in cells of the secondary xylem (Metcalfe & Chalk, 1950: 1354). Raphides are reported for secondary phloem of *Calycopteris* (Combretaceae), however (Metcalfe & Chalk, 1950). Obviously, raphides have evolved polyphyletically in various lines of angiosperms, and the shift from numerous prismatic crystals within a cell to raphides is not, probably, as sharp a transition as we might imagine. Coarse raphides can be termed prismatic crystals. Coarse raphides can be observed in species of *Gaura*, such as *G. villosa* subsp. *villosa* (Fig. 38), or in *Oenothera linifolia* (Fig. 50). Such coarse raphides are wider and less numerous, but may still occur many to a cell.

Cells containing raphides can occur idioblastically in fascicular xylem of Onagraceae. Such cells may be thin or thick walled: they may even resemble fibers in respects other than shape and cell contents. Most commonly, however, cells containing raphides occur in vertical pairs (Figs. 4, 12, 44); they are relatively thin-walled with blunt ends compared to fibers, and represent the product of a transverse division of a fusiform cambial initial derivative. Metcalfe & Chalk (1950) find that cells containing raphides in Onagraceae are commonly rich in mucilage, and my findings tend to support this. Occurrence of raphides in single fiber-like cells rather than in paired cells was observed in *Oenothera linifolia.* Because idioblasts containing raphides, even though fiber-like in shape and even wall characteristics, could be classified as parenchyma, one might say that diffuse occurrence of such cells in fascicular xylem constitutes presence of diffuse parenchyma. If so, one must be careful to state that this is not diffuse parenchyma in the ordinary sense in which that word is understood, as in the diffuse parenchyma of primitive dicotyledon woods.

Where parenchyma is abundant in interxylary phloem bands, as in some Lopezieae, idioblasts containing raphides tend to occur in that parenchyma (Figs. 12, 43–44, 48). These cells tend to be broader than ordinary phloem parenchyma cells or the fiber-like cells that contain raphides; they commonly occur in vertical pairs because of the presence of a transverse wall. Raphides tend to be needle-like in these species.

Occurrence of raphides in rays was observed in *Gaura villosa* subsp. *villosa* (Figs. 37–38) and *Xylonagra arborea* subsp. *wigginsii.*



FIGURES 43–46. Wood sections of *Lopezia lopezioides, Breedlove 8052*.—43. Transection of parenchyma band, photographed with partially polarized light. Raphides in transection (lower left); starch grains show bright patterns.—44. Tangential section of parenchyma band. Raphides within two pairs of cells and a single cell; starch grains in the other cells are visible. —45. Parenchyma cells from tangential section. Vessels are to right and left, and beginnings of tyloses intruding into these from axial parenchyma cells can be seen.—46. Tangential section; portion showing starch grains in parenchyma cells of a band of parenchyma. [Magnification scale for Figs. 43, 45–46 shown below Fig. 18; scale for Fig. 44 below Fig. 15.]

In viewing the distribution of raphides within the family (Table 1), one notes that they occur in woods of all tribes except Jussiaeeae and Epilobieae; only a few species in each of those two tribes were examined, so absence is not yet certain. Absence of raphides in wood of a particular onagraceous species is probably a rather casual matter. In Onagraceae, raphides may be present elsewhere in the plant body even if absent in wood. The occurrence of raphides in fiber-like fascicular cells in *Fuchsia* and *Hauya* as well as in Onagreae indicates a basic unity among woods of Onagraceae. Lopezieae in this study were not observed to possess raphides in fiber-like cells, but one must take into account that the relatively abundant parenchyma of the interxylary phloem bands provides an ideal alternative site for deposition of raphides, and that this tissue is not present in *Fuchsia* or *Hauya*. The occurrence of raphides in three types of cells in *Gaura villosa* subsp. *villosa* demonstrates the versatility in mode of occurrence that can occur in Onagraceae. Systematic and organographic distribution of raphides in Onagraceae is undoubtedly greater than present reports indicate.

Prismatic Crystals.—Prismatic crystals in Onagraceae are not diamond-shaped or rhombohedral, but rather, where they can be clearly seen, tend to take elongate forms, bluntly pointed at one end, indented at the other end (Figs. 26, 41–42). Such prismatic crystals were observed in only a few species. They are most clearly displayed in rays of *Ludwigia octovalvis* (Fig. 26), in which usually only a single crystal per ray cell is present.

Gaura sinuata (Fig. 40) and *G. villosa* subsp. *villosa* present a distinctive mode of prismatic crystal occurrence. In these two species, prismatic crystals of various sizes occur in fibers. These fibers are distributed idioblastically within fascicular xylem, and are non-septate.

Hauya also has prismatic crystals within fibers (Figs. 41–42), but in a mode of occurrence unlike that of *Gaura*. In *H. elegans* subsp. *cornuta*, the fibers that contain prismatic crystals are markedly widened to accommodate the large size of the prismatic crystals. These prismatic crystals most commonly occur one to a fiber (Fig. 42), ocasionally two (Fig. 41). In either case, each prismatic crystal is encapsulated by a lignified secondary wall, which appears to sheathe the crystal closely leaving little or no additional space. In such crystal-containing fibers, a few small crystal fragments can be seen above or below the large encapsulated prismatic crystal (Fig. 42, above). The large prismatic crystals of *Hauya* are termed styloids by Metcalfe & Chalk (1950).

The mode of prismatic crystal occurrence in *Hauya* and, to a lesser extent, *Gaura* is similar to that in *Punica granatum*. In this species, prismatic crystals occur in fibers, but these fibers are septate (with thin, non-lignified walls as septa) in such a way that usually only one crystal per chamber occurs (Metcalfe & Chalk (1950: 642; also confirmed by my own observations). The same condition has been reported for some Combretaceae (Solereder, 1908), certain Myrtaceae (Metcalfe & Chalk, 1950), and three genera of Lythraceae (Metcalfe & Chalk, 1950). This highly distinctive mode of crystal occurrence would seem a good indicator of relationships among these families.

Prismatic crystals in rays, perhaps like those of *Ludwigia*, have been reported

by Metcalfe & Chalk (1950) for *Sonneratia* of the Sonneratiaceae; for several genera of Combretaceae; for *Calyptranthes* of Myrtaceae, and for several genera of Lecythidaceae (Metcalfe & Chalk, 1950). These reports of ray crystals may be considered a subsidiary indicator of relationships of Onagraceae.

UNIDENTIFIED DEPOSITS

Many Onagraceae, particularly perennials and those of drier areas, characteristically possess deposits, which range from grayish and granular, suggesting tannins; to dark, solid and gummy materials, present as droplets or massive accumulations occluding lumina. The latter gummy type of deposit is abundantly represented in Onagraceae. It was observed in *Calylophus hartwegii* subsp. *pubescens* (fibers), *C. serrulatus* (fibers), *Gaura sinuata* (rays, fibers: Fig. 40), *G. villosa* subsp. *villosa* (rays, fibers: Fig. 35), *Gongylocarpus fruticulosus* subsp. *glaber* (all cell types: Carlquist & Raven, 1966), *Lopezia semeiandra* (some ray cells), *L. grandiflora* (some ray cells, fibers: Fig. 14), *Ludwigia octovalvis* (rays: Fig. 26), *L. uruguayensis* (rays, fibers: Figs. 23–25), *Oenothera linifolia* (ray cells: Figs. 29, 30), and *Xylonagra arborea* subsp. *wigginsii* (ray cells: Figs. 31–33). Small droplets of these substances can be seen in almost any wood of Onagraceae.

These deposits are termed "dark gummy" materials by Metcalfe & Chalk (1950). Those authors reported them for the myrtalean families Combretaceae (notably *Lumnitzera*), Crypteroniaceae, Lecythidaceae, Lythraceae, Melastomaceae, and Myrtaceae. The chemical nature of these deposits has not, to my knowledge, been analyzed to see if they represent, in fact, similar compounds in the families named.

GROWTH RINGS

Various types of growth-ring phenomena have been mentioned above, such as the occurrence of gelatinous fibers. Biennial stems, or annual stems that have evidently responded to seasonality, as in the sample of *Oenothera linifolia* studied, may show a parenchymatous cylinder interpolated into the wood. Fluctuations of seasonal moisture availability seem obviously related to fluctuations in vessel diameter within wood samples. No growth rings in the Onagraceae studied appear to be at all obligate, however.

Moss (1936) has discussed occurrence of interxylary cork, a growth-ring phenomenon with obvious and interesting ecological correlations, in *Epilobium angustifolium* L. No such interxylary periderm formation, however, was present in any of the samples of Onagraceae I have studied.

PHOTOSYNTHATE TRANSFER AND STORAGE ALTERNATIVES

The presence in so many Onagraceae of starch grains and of interxylary phloem demands explanation. Too often, wood anatomists have considered the xylem a tissue of water transport and neglected consideration of photosynthate conduction and storage within secondary xylem. As Braun (1970) has shown, even species of tropical environments store and mobilize starch within wood. However, season-

ality or periodicity in growth flushes or in flowering and fruiting are definitely present in tropical plants and relate to storage of starch or sugar.

In the case of Onagraceae, flowering frequently takes place in the dry season. As one example, I have seen *Fuchsia cyrtandroides* on Tahiti during July, the dry season, flowering on branches that are virtually leafless. The data of Plitmann, Raven & Breedlove (1973) show that Lopezieae mostly flower during the dry season, although sporadically at other times of the year. Even such annuals as *Oenothera* and *Clarkia* may grow during the winter rainy season but not flower until much later. *Oenothera* and *Camissonia* often form prominent leaf rosettes or large basal leaves during winter months. They can be presumed to store starch during winter and spring, and mobilize it in late spring when they flower—at which time basal leaves may have withered. Therefore storage of starch in the stem during the vegetative period is understandable.

As mentioned above, some annual Onagraceae lack interxylary phloem. In them, secondary phloem plus intraxylary phloem suffice for conduction of sugars: the intervening secondary xylem is, presumably, not wide enough to provide selective value for interpolation of interxylary phloem strands. Libriform fibers in the annuals, as in all Onagraceae, are of protracted longevity, so that the fascicular xylem can be considered vessels embedded within a fibriform parenchyma.

Larger annuals, in which considerable secondary xylem develops, may have interxylary phloem, as in species of *Camissonia*, *Oenothera*, and *Gaura*. In these, selective pressure for occurrence of interxylary phloem may be based on spatial considerations: it would provide more numerous conduits for rapid input into and removal of sugars from starch-storing fibers. One may also hypothesize that interxylary phloem is present in some annuals as a derivation from perennial ancestors with wider stems, in which case the phloem would be of no negative value.

Considerations such as the above—increased number of photosynthate-conducting conduits—may apply to perennials like *Lopezia* (sens. lat.), *Gaura*, *Gongylocarpus fruticulosus*, *Xylonagra*, and *Zauschneria*. In these, interxylary phloem in older portions of stems might be expected to be deactivated eventually, if not annually, so that formation of additional strands of interxylary phloem would be of functional value. Noteworthy in some woody perennials is that they form massive displays of flowers, or have large flowers (*e.g.*, *Lopezia longiflora*). Production of large flowers or large quantities of flowers during a short period might be related to massive starch reserves and to interxylary phloem for rapid transport of sugars. The large phloem-containing bands of *Lopezia longiflora* may serve for storage of water, as well as starch, preparatory to flowering.

With *Fuchsia* and *Hauya*, we are dealing with shrubs and trees with less seasonality in growth and flowering. In these, starch storage is never as conspicuous as in, say, Lopezieae. Seasonality does occur but slow rates of input and mobilization of photosynthates within wood may be hypothesized because of longer flowering seasons or longer vegetative seasons. If so, lack of abundance of starch and lack of interxylary phloem in these two genera is explainable. The

FIGURES 47–50. Wood sections of Onagraceae to show various histological details.—47. *Lopezia longiflora*. Portion of a tangential section. Starch-filled septate fiber, center.—48. *Lopezia miniata* subsp. *miniata*. Transection, photographed with polarized light. Packet of raphides, above left, is in a band of phloem-bearing parenchyma. Starch is abundant in libriform fibers, walls of which are birefringent.—49. *Fuchsia tuberosa*. Transection from periphery of secondary xylem. Pitted vasicentric parenchyma cells surround vessel at upper left. Thin-walled axial parenchyma cells scattered among libriform fibers in upper half of

presence of relatively abundant vasicentric parenchyma and of the apotracheal bands of parenchyma in *Hauya* are ideal alternatives to interxylary phloem where vertical conduction of photosynthates is concerned. Storage of starch in rays in *Hauya* suggests a site of deposition from which photosynthates could be mobilized and transported quickly to axial parenchyma. In *Fuchsia*, vasicentric parenchyma is scanty, and no apotracheal parenchyma bands are present. However, rays are exceptionally tall in *Fuchsia*, with numerous erect cells. These cells are functionally similar to axial parenchyma and can be hypothesized to serve for photosynthate translocation where rates are slow.

Ludwigia may form a special case, in that it can develop (*L. octovalvis*) rather large woody stems without interxylary phloem (although *Ludwigia* never forms trees, and can be called shrubby only in a special sense). Because *Ludwigia* characteristically grows in very wet or inundated soil, plants experience minimal seasonality: the vegetative phase is not abruptly terminated prior to flowering, and plants typically flower and form new leaves concurrently. Thus, mobilization of starch need not be rapid. Interestingly, rays are extremely tall in *Ludwigia* (see Table 1), so that as in *Fuchsia*, the numerous erect ray cells may well take the place of axial parenchyma and interxylary phloem, and low rates of photosynthate conduction can be hypothesized, as in *Fuchsia*.

I have noted elsewhere (Carlquist, 1975) the striking correlation between lack of axial parenchyma and presence of septate or nucleate fibers in dicotyledon families. The respective lists of families with little or no axial parenchyma, and with septate or nucleate fibers are very similar, so that a functional correlation appears probable. The correlation would be that living fibers serve for storage and conduction of photosynthates, so that the imperforate elements of the xylem serve much as a total parenchyma background in the wood, yet offer greater mechanical strength than would the equivalent amount of thin-walled parenchyma.

Erect ray cells (the "contact cells" of Braun, 1970) can be considered a substitute for axial parenchyma to some degree, serving for vertical as well as lateral conduction of photosynthates in woods with little or no axial parenchyma. If ray cells are predominantly erect, as they are in nearly all Onagraceae as well as in many species of other myrtalean families (see above), there exists a ray system ideal for vertical translocation. I have commented earlier (Carlquist, 1962) on the tendency of ray cells to be predominantly erect in herbaceous and herb-like plants, and discussed this in terms of retardation of transverse subdivision of ray initials in the cambium. In ontogenetic terms, this certainly appears to be true. I have not hitherto commented on the possible functional significance of this juvenilism. On the basis of Onagraceae, the explanation would appear to lie in assumption by rays of the dual roles of lateral and vertical conduction of photosynthates within secondary xylem. Where stems grow slowly, as in rosette trees,

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photograph. Starch grains are present in many of the fibers.—50. *Oenothera linifolia*. Transection. Older portion of xylem, showing thick-walled sclereids derived from phloem parenchyma. Three raphide-bearing cells are visible. [Magnification scale for Figs. 47, 49–50 shown below Fig. 18; scale for Fig. 48 below Fig. 15.]

value of efficient lateral translocation of photosynthates is lessened, although there is still a strong value in favor of efficient vertical translocation. This would correspond to the relative abundance of erect ray cells. I propose this as an addendum to my hypothesis concerning parenchyma function and juvenilism in my 1975 essay.

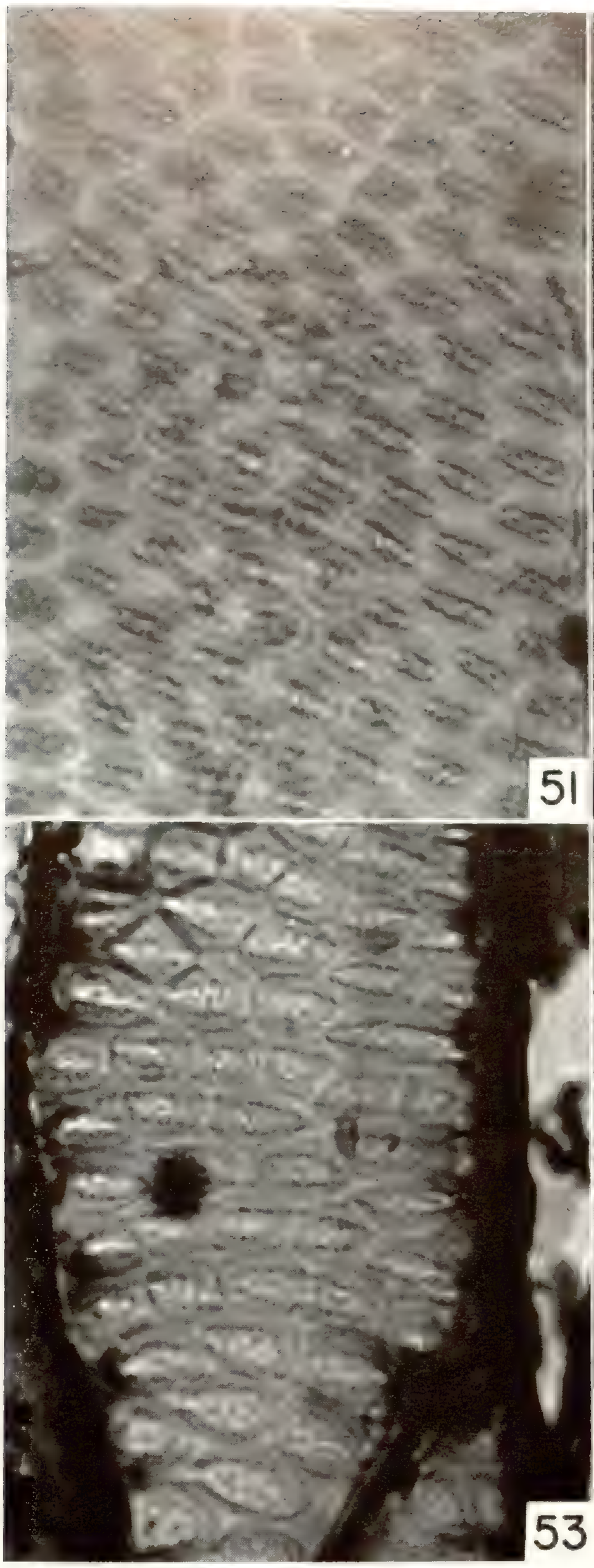
In Onagraceae, a dramatic example in shift of cell types in rays can be seen in *Hauya*. At first, erect ray cells predominate, but later, procumbent cells are at least as abundant. In large stems, such as those of the genus *Hauya*, larger quantities of procumbent cells to facilitate radial translocation could be expected.

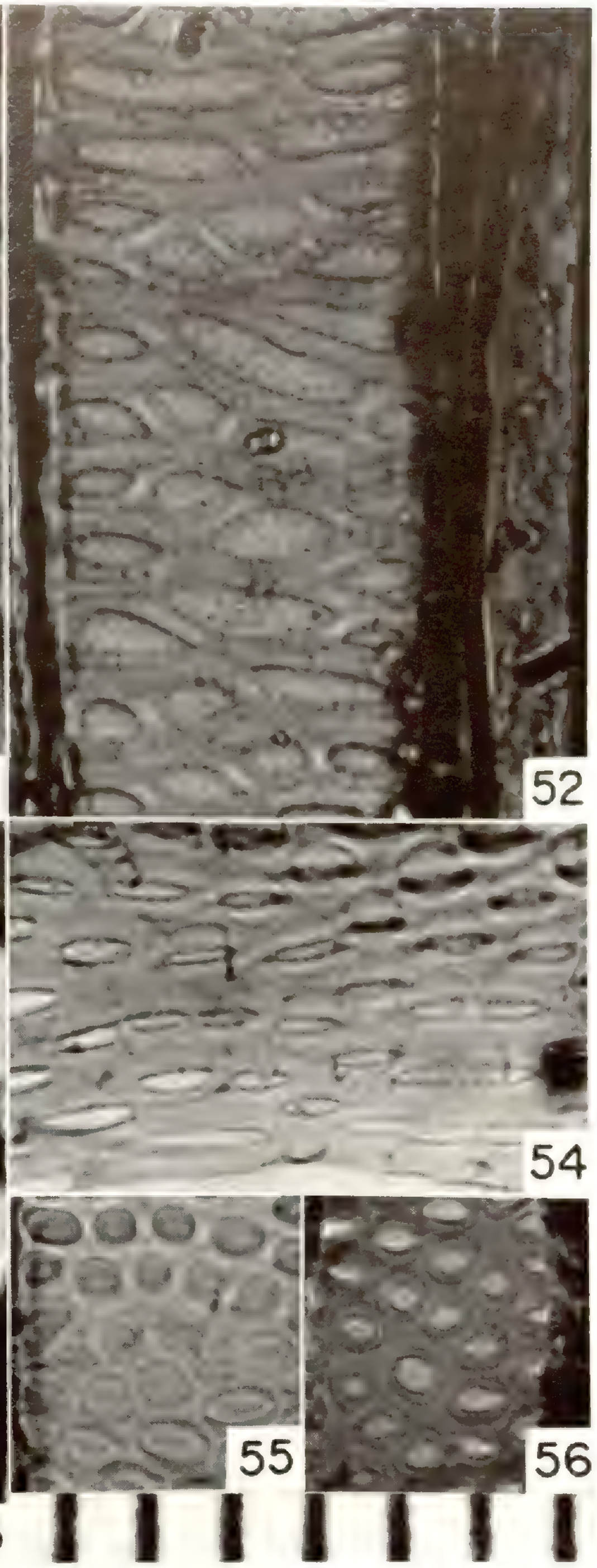
The above hypothesis is obviously based on the assumption that cell walls operate as deterrents to conduction within rays, so that cells elongating in the direction of putative conduction would therefore present fewer impedances per unit length. This assumption runs parallel to formulas on the impedance provided in the case of water conduction by end walls of tracheids (see, for example, my 1975 discussion of gymnosperm woods).

Growth Form and Wood Anatomy

The discussion above, albeit hypothetical, includes consideration of growth form. With respect to other features, one can say that the relatively thin-walled nature of libriform fibers and gelatinous nature of fiber walls in Onagraceae seem related to limited plant stature. Also, the presence of elongate pits and of pits with large, gaping apertures suggests low mechanical strength, characteristic of herb-like plants (Carlquist, 1975). A minimal degree of gelatinous fiber formation, together with relatively thick-walled fibers, occurs in *Hauya* (Figs. 6–7). This is true, to a lesser degree, also of *Fuchsia*.

Of what significance is occurrence of interxylary phloem in ancestors of Onagraceae? What growth form is ancestral for Onagraceae? To be sure, interxylary phloem is present, as noted above, in some Melastomaceae and some Combretaceae, but is known from Lythraceae only in the instance of *Lythrum salicaria*. It is otherwise absent from Lythraceae and it is absent in Punicaceae, Crypteroniaceae, and Sonneratiaceae—which would seem to be a trio of families close to Onagraceae—as well as Myrtaceae, Penaeaceae, Oliniaceae, and Lecythidaceae. One is tempted to say that if woody forms are ancestral in Onagraceae, absence of interxylary phloem in those ancestors is likely. Polyphyletic origin of interxylary phloem produced by a single cambium (the "foraminate" type of Metcalfe & Chalk, 1950) must be hypothesized to account for systematic distribution of this phloem type in at least non-myrtalean families and very likely myrtalean families also. The fact that intraxylary phloem (which also occurs in a variety of dicotyledon families, not all of which form a natural group) is present in Onagraceae suggests an increase in phloem dispersion within the plant body, a tendency that might be converted, via cambial action, into formation of interxylary phloem independently within Myrtales. Because no tribe of Onagraceae has interxylary phloem in all species, one would have to hypothesize polyphyletic loss of interxylary phloem if one assumed interxylary phloem was present ancestrally in Onagraceae. This seems somewhat more difficult than the reverse





FIGURES 51–56. Details of intervascular pitting from tangential sections of wood of Onagraceae.—51. *Fuchsia paniculata*. Circular and elliptical vestured pits.—52. *Lopezia langmaniae*. Pits are large and vestured.—53. *Lopezia lopezioides*. Pits are crowded, vestured.—54. *Lopezia longiflora*. Pit cavities are circular, but apertures tend to be grooves, as shaved-away portions of vessel wall, below, shows. Vesturing is evident.—55. *Lopezia miniata* subsp. *paniculata*. Pits are circular; vesturing obscure.—56. *Oenothera deltoides* subsp. *howellii*. Pits are circular with wide apertures; no vesturing evident. [Magnification scale for Figs. 51–56 shown at bottom right; divisions = 10 μ.]

hypothesis: ancestral absence but potential for interxylary phloem formation. Either hypothesis is still conceivable on the basis of data now available.

The absence of interxylary phloem in the common ancestor of Onagraceae is also suggested by relationships within the family as judged by other characteristics. Morphologically and in terms of floral anatomy, *Fuchsia* and *Ludwigia* are the most generalized members of the family (Eyde & Morgan, 1973), and *Hauya* is clearly one of the most, if not the most, generalized of the assemblage of genera assigned to the tribe Onagreae by Raven (1964), among which it is unique in its possession of stipules. Judged by any criteria, the remaining Onagreae, the Lopezieae, and the Epilobieae are more advanced (Peter H. Raven, personal communication), and these are the groups in which interxylary phloem has evolved. Links between Lopezieae and *Ludwigia* (Eyde & Morgan, 1973) and between Onagreae sens. str. and *Hauya* suggest that interxylary phloem has evolved more than once within Onagraceae, as does the apparent lack of any direct relationship among the three tribes in which it occurs.

With respect to growth form, Onagraceae show woods with herbaceous modes of structure in herbaceous species. However, in the shrubby and arboreal genera *Fuchsia* and *Hauya*, there are no vestiges of what I would term herbaceous structure. By "vestiges of herbaceous structure" I mean largely features such as those I cited in my 1962 paper (Carlquist, 1962), but also modes of structure described in Goodeniaceae (Carlquist, 1969*a*) and Campanulaceae (Carlquist, 1969*b*), families that seem ancestrally herbaceous but with some species forming shrubs or trees as large as Onagraceae, with the exception of *Hauya*. There are no indicators of herbaceous modes of structure in *Punica* or Sonneratiaceae, although Lythraceae obviously contain a variety of growth forms (the woodier ones seem non-herbaceous in wood structure, however). As an intuitive speculation, I would hypothesize a shrubby growth form, but one from which more herbaceous growth forms could easily be derived, as ancestral to Onagraceae. Even if this were the case, one could hypothesize secondary increase in woodiness (*Lopezia*? *Ludwigia*?) within the family. No single genus of Onagraceae seems clearly to have a preponderance of features definitely primitive for the family.

RELATIONSHIPS OF ONAGRACEAE

As the text above suggests, anatomical features prove unusually decisive in establishing relationships of Onagraceae. Affinities seem greatest with Lythraceae, Punicaceae, Sonneratiaceae, Crypteroniaceae, and Combretaceae. In fact, those families with the exception of Combretaceae could, with justification, be united into Lythraceae (Robert F. Thorne, personal communication), in which case Onagraceae could be said to be most closely allied to Lythraceae (sens. lat.) and to Combretaceae. Other myrtalean families, such as Melastomaceae, have nearly as many features in common with Onagraceae. Anatomical features one can cite include presence of vestured pits on vessel walls; occurrence of intraxylary phloem adjacent to primary xylem; ray cells square to erect predominantly or exclusively; vasicentric parenchyma scanty; libriform fibers with non-bordered pits, and often septate or nucleate; prismatic crystals present in ray cells or

chambered within septate fibers; dark gummy deposits present in ray cells and in other xylem cells. On the basis of wood anatomy alone, affinities of the family Onagraceae are easy to establish compared with most phylogenetic problems. That Onagraceae could have so many unusual wood features in common with the families listed cannot be explained by parallelism, but only by true relationship.

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ANATOMICAL COMPARISONS OF FIVE SPECIES OF *OPUNTIA* (CACTACEAE)[1]

Louis F. Conde[2]

Abstract

Five species of the genus *Opuntia* were studied with respect to several characteristics; cuticular thickness, epidermal papillosity, stomatal size and frequency, hypodermal thickness, vessel member dimensions, and relative succulence. The five species comprise three growth forms: pencil chollas (*O. leptocaulis*, *O. kleiniae*), tree chollas (*O. imbricata*) and prickly pears (*O. phaeacantha*, *O. lindheimeri*). The three chollas are members of the subgenus *Cylindropuntia*, while the two prickly pears are members of the subgenus *Opuntia*.

On the basis of the five species examined in the study, each of the three growth forms, pencil chollas, tree chollas, and prickly pears, is distinct with respect to the degree of papillosity of the epidermal cells, hypodermal thickness, and vessel width. In addition, the two subgenera are distinct with respect to cuticular thickness.

Characteristics showing the least variability within a species are stomatal length and vessel member dimensions. Characteristics showing the most variability within a species are cuticular thickness, stomatal frequency, and stomatal index. Overall, no one species, growth form or subgenus is more variable than any other.

Cacti, and succulents in general, are essentially living reservoirs of water. The ability of the Cactaceae to inhabit arid or semi-arid regions is due primarily to this capacity for water storage (Preston, 1901; Bédélian, 1911; Boosfeld, 1920; Bailey, 1968). As has been pointed out by Pisek & Berger (1938), cacti are not drought resistant in the sense of being able to recover from a severe water deficit, rather their resistance is due to the fact that they do not dry out readily. It is among the true xerophytes, such as creosote bush (*Larrea*) (Runyon, 1936), and some vascular cryptogams, that the greatest resistance to extreme water deficits is seen. Many of the modifications seen in the Cactaceae serve to facilitate uptake or storage of available water or retention of absorbed water. These modifications may be physiological, morphological, or anatomical.

Physiological modifications occur in both stem and root. Kausch (1965), for example, has indicated that there is a very rapid resumption of activity in the roots in response to watering after a prolonged drought. The nocturnal opening of the stomates (Nishida, 1963) is an adaptation which would decrease the rate of water loss during gas exchange. There is, however, some doubt as to the universality of this stomatal phenomenon in the Cactaceae (Holdsworth, 1971).

Morphological modifications include tendencies for the plant body to be

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[1] I would like to mention a few of the many people who have given their help at one time or another during the course of this study. Dr. Richard A. White, my major professor, has been understanding and helpful in many ways throughout the study. Drs. Donald E. Stone and Paul J. Kramer contributed significantly to the completion of the dissertation. Dr. Lyman Benson of Pomona College was kind enough to annotate the plant collections used in the study.

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massive, as in the saguaro (*Cereus giganteus* Engelm.) or compact and globular, as in *Mammillaria*. Either of these modifications results in less evaporating surface per unit volume of the plant body than would be the case for the shrub or tree forms possessed by the more primitive leaf-bearing cacti. Absorbing portions of the root systems tend to be shallow and widespread, which would facilitate rapid uptake of available water (Preston, 1900; Cannon, 1911; Markle, 1917).

The anatomical modifications of the Cactaceae are relatively well known due to a number of survey studies dating from the middle of the nineteenth century (Schleiden, 1845; Ganong, 1895; Bédélian, 1911; Gravis, 1935). There were, however, two basic problems with the early works. Nearly without exception cultivated materials were used and thus only one or a very few individuals of each species were studied. The use of small samples meant that little was discovered about populational variability for a given character. Since the material was cultivated, nothing was learned about environmental variability for a given character. Many of the early authors emphasized the necessity of using material from its natural habitat (Ganong, 1895; Boosfeld, 1920), stating that the anatomy of the cultivated plants was very likely different in some respects from the anatomy of plants in their natural habitat.

The early surveys did show that there were great differences in internal anatomy among different genera and different species. Some authors, particularly Boosfeld (1920), emphasized the correlation of internal anatomy with external form, noting that taxa that had very different forms also had very different internal structure. It does seem reasonable that different anatomical features might have developed in plants with different growth forms in response to an arid environment. The relationships of the internal structure to the external form was unclear, partly because the plants compared were often not closely related, and partly because the plants compared were often not adapted to the same habitat. Each of the North American deserts, for example, is quite distinct (Shreve, 1942). When the South American deserts and the Central and South American wet forests are also taken into account, it can be seen that the Cactaceae embrace considerable habitat diversity. By comparing closely related plants occupying the same habitat, rather than distantly related plants from different habitats, some indication of the relationship of external form to internal structure might be obtained.

The genus *Opuntia* was chosen for the present study because several distinct growth forms occur in North America. The pencil chollas, in the subgenus *Cylindropuntia*, are bushy or shrubby plants with thin, more or less fleshy, cylindrical stems. The tree chollas, also in the subgenus *Cylindropuntia*, are bushy or shrubby plants with thicker, more or less fleshy, cylindrical stems. The prickly pears, in the subgenus *Opuntia*, are bushy or shrubby plants with stems comprised of fleshy, oval, flattened pads.

Representatives of the three growth forms commonly occur in association in nature, thus decreasing the effects that different habitats might have on anatomy. The five species of *Opuntia* used in this study are relatively widespread in the southwestern United States and north-central Mexico, thus enabling field collec-

tions over a wide geographic range and providing an indication of the anatomical variability among natural populations. Anthony (1954, 1956) states that species of prickly pears tend to be morphologically more variable than species of chollas. It is not known if this is also true of the anatomical characteristics.

The characters which were examined in this study are epidermal papillosity, cuticular thickness, stomatal size and frequency, hypodermal thickness, and vessel member dimensions. Bailey (1964*b*) found in his studies of the pereskiads and their nearest relatives "that a preliminary investigation of the cuticle, epidermis, stomatal apparatuses, and subepidermal layers of the most primitive surviving representatives of the Cactaceae reveal salient trends of structural specialization whose functional significance can be fully and reliably elucidated only by sustained experimental and other observations on plants growing in their native habitats. Such detailed experimental investigations, in adequate correlation with anatomical and environmental ones, are at present much needed for a clearer understanding of salient adaptations in the Cactaceae which are essential for survival in arid environments." The opuntiads, presumably derived from the pereskiads, should show extensions of the "trends of structural specialization" seen by Bailey. The functional significance of such specializations is still to a great extent speculative.

Thus, the present study had three main goals: (1) to determine any differences between the three morphological forms and/or the two subgenera with respect to the characteristics considered; (2) to determine the amount of variability among individuals within a species with respect to the characteristics considered; and (3) to determine if these characteristics show continuations of the trends of specialization seen in the pereskiads by Bailey.

Materials and Methods

The taxa used in this study were *Opuntia leptocaulis* DC. (12 collections), *O. kleiniae* DC. (5 collections), and *O. imbricata* (Haw.) DC. (17 collections), all of the subgenus *Cylindropuntia*; and *O. phaeacantha* Engelm. (4 collections), and *O. lindheimeri* Engelm. (11 collections), both of the subgenus *Opuntia*. Thus there were 34 collections representing three species of subgenus *Cylindropuntia* and 15 collections representing two species of subgenus *Opuntia*.

The following brief morphological descriptions are based on the species descriptions of Britton & Rose (1937) and Benson (1969).

Opuntia leptocaulis (pencil cholla)—Bush or erect small shrub; main trunk, if present, very short; joints cylindric, elongate, 30–40 cm long; lateral joints much shorter than the main branches, cylindric, 2.5–7.5 cm long, about 3.0–8.0 mm in diameter; tubercles almost lacking; the stem nearly smooth.

Opuntia kleiniae (pencil cholla, Fig. 3)—Bush or shrub, 0.3–2.2 m high; stems branching divergently; joints cylindric, elongate, 10–30 cm long, 6.0–10.0 mm in diameter; tubercles prominent.

Opuntia imbricata (tree cholla, Fig. 2)—Small tree, arborescent plant, or thicket-forming shrub, usually 0.9–3.0 m high; trunk short, branches much longer; joints 12–38 cm long, 19.0–32.0 mm in diameter; tubercles very prominent.

FIGURE 1. Distribution of collection sites in Mexico and the Big Bend region of Texas.

Opuntia lindheimeri (prickly pear, Fig. 4)—Erect or occasionally spreading plant, up to 2 m high; sometimes with a short main trunk; joints orbiculate to obovate, 15–25 cm long, 13–23 cm broad.

Opuntia phaeacantha (prickly pear, Fig. 5)—Large prostrate or sprawling plant, forming clumps 0.6–2.5 or even 6 m in diameter and 30–90 cm high; trunk none; joints obovate to orbiculate, 10–15 or even 25 cm long, 7–23 cm broad.

Collections were made during July and early August of 1969 in an area extending from southern Texas to central Mexico. In order to make interspecific comparisons more valid, localities where several species were growing in association were selected whenever possible. The 49 collections were made at 21 sites (Tables 1–2; Fig. 1). Samples of the stems of each collection were preserved in formalin-acetic acid-alcohol (FAA). Voucher specimens of each collection are on deposit in the Duke University Herbarium (DUKE).

Blocks of tissue from each of the preserved samples were dehydrated in an absolute ethanol-chloroform series (Purvis, Collier & Walls, 1964) and embedded in 61° C Tissuemat. Serial longitudinal and transverse sections 10 μ in thickness were cut on a rotary microtome, stained in safranin-fast green and mounted in Piccolyte.

In order to obtain epidermal peels, small blocks of tissue comprised of the

TABLE 1. Locality data for collection sites.

Site	Location
1	TAMAULIPAS: 38.2 km S of Nuevo Laredo on México 85, dry roadside scrub, 206 m elevation.
2	NUEVO LEÓN: 11.7 km S of Sabinas Hidalgo on México 85, roadside among Acacias, 610 m.
3	NUEVO LEÓN: 36 km W of Linares on México 60, dry scrub, 1100 m.
4	NUEVO LEÓN: N side of México 60, 1 km E of junction with Galeana road, 1680 m.
5	TAMAULIPAS: 56.8 km SW of Ciudad Victoria on México 70 to Juamave, fine sandy soil, open scrub, 760 m.
6	TAMAULIPAS: 59.7 km SW of Ciudad Victoria on México 70 to Juamave, fine sandy soil, open scrub, 700 m.
7	TAMAULIPAS: México 70, 57.5 km N of intersection with México 80, high plain, 1340 m.
8	SAN LUIS POTOSÍ: On México 80, 6.6 km E of intersection with México 70, 1070 m.
9	HIDALGO: 60 km N of Ixmiquilpan on México 85, steep hillside with some pines, 1840 m.
10	HIDALGO: 20.4 km N of Ixmiquilpan on México 85, 1620 m.
11	HIDALGO: Vacant lot on edge of town of Lagunilla, 24.6 km S of Ixmiquilpan on México 85, 1860 m.
12	AGUASCALIENTES: Scrub on south side of México 70, 9.2 km E of main square in city of Aguascalientes, 2010 m.
13	SAN LUIS POTOSÍ: 1.6 km S of the San Luis Potosí–Nuevo León state line on México 57, 1600 m.
14	COAHUILA: On México 40, 18.5 km W of junction with Parras road, 1040 m.
15	CHIHUAHUA: On México 49, 22.8 km N of Durango–Chihuahua state line near km post 67, 1220 m.
16	CHIHUAHUA: On Chihuahua 22, 25.1 km S of intersection with México 45 in Ciudad Camargo, 1220 m.
17	CHIHUAHUA: 40 km S of Chihuahua on México 45, grassy flats, 1170 m.
18	TEXAS: Big Bend National Park, 7.4 km E of Panther Junction on road to Rio Grande Village, 1070 m.
19	TEXAS: Big Bend National Park, 2.3 km S of Basin Junction on Basin Road, 1390 m.
20	TEXAS: Big Bend National Park, 1.6 km E of Maverick on W edge of the park, 930 m.
21	TEXAS: Big Bend National Park, 13 km S of junction of Castolon road with Panther Junction–Maverick road, grassy slopes, 1340 m.

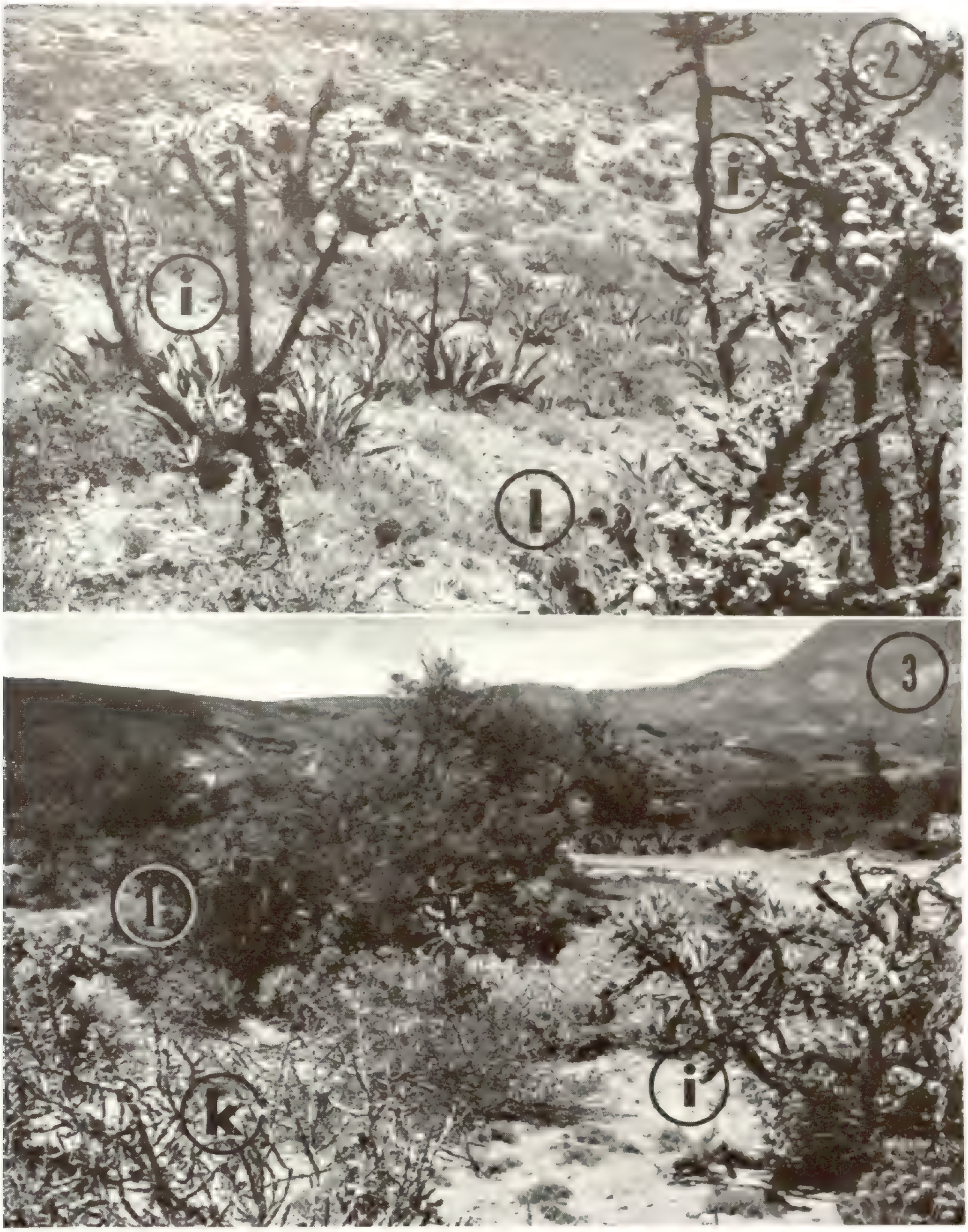
epidermis and adjacent cortical tissues were soaked in Jeffrey's solution (equal parts of 10% chromic and 10% nitric acids) for about an hour or until all the subepidermal tissues could be readily separated from the epidermis. The isolated epidermis was then washed in water, rinsed in absolute ethanol, stained in Sudan IV in absolute ethanol and mounted in glycerine on a glass slide.

Wood macerations were prepared by soaking pieces of the oldest wood available in Jeffrey's solution until the wood was soft and pliable, usually 36 hours or more. These pieces were washed in running water until all visible traces of the

TABLE 2. Individuals collected at each site.

Species	Site																				
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21
O. leptocaulis	×[a]	×	×	×	×	×	×	×						×				×		×	
O. kleiniae								×		×	×		×				×		×		
O. imbricata			×	×[a]		×		×	×	×	×	×	×	×	×	×	×	×	×		×
O. lindheimeri	×[a]	×	×	×				×	×	×	×							×[a]			
O. phaeacantha														×		×			×		×

[a] Two individuals of the species were collected.



FIGURES 2–3. Collection sites for *Opuntia* species.—2. Site 4, showing *O. imbricata* (i) and *O. lindheimeri* (l).—3. Site 10, showing *O. kleiniae* (k), *O. imbricata* (i) and *O. lindheimeri* (l) in the left center.

acid were removed. They were stained overnight in a 1% solution of safranin in 50% ethanol. The stained pieces were then teased apart, washed in absolute ethanol and then washed in xylene before mounting in Piccolyte.

Whole transverse sections were made of the stem of each specimen, bleached in a 5% solution of Clorox, washed in water, stained in a 0.005% solution of safranin in 50% ethanol and destained in 50% ethanol. These sections were then photo-

FIGURES 4–5. Collection sites for *Opuntia* species.—4. Site 11, showing *O. kleiniae* (k), *O. imbricata* (i) and *O. lindheimeri* (l).—5. Site 19, showing *O. imbricata* (i) and *O. phaeacantha* (p).

graphed using transmitted light and Kodak Panatomic X or Ektapan sheet film. The negatives were enlarged and printed on Kodak Polycontrast paper. The circumference and area of the sections were measured from the photographs using a Compass map measurer and a Keuffel and Esser compensating polar planimeter respectively.

Segments of the species collected in Texas were brought back to Duke

University and grown in the greenhouse. Root tips from these plants were treated in a 0.1% solution of colchicine for 4–5 hours, and then killed and fixed in a 3/1 mixture of absolute ethanol and glacial acetic acid. Root tips were hydrolyzed for 10–12 minutes in 1N HCl and then stained and squashed in aceto-orcein. Photomicrographs of the chromosome preparations were taken with a Leitz Ortholux microscope on Kodak High Contrast Copy film.

Photomicrographs of sectioned material, epidermal peels, and wood macerations were taken with a Leitz Ortholux microscope on Kodak Panatomic X roll film.

The bulk of the manipulations of the data were done on an IBM S/360 Model 40 computer at the Duke University Computation Center.

Results

The overall comparisons (Table 3) indicate the average value and the amount of variation of each character over the entire range of collection sites for each species. These results are thus influenced by the environmental differences among the various sites as well as the genetic difference between individuals. While very large habitat differences can and do exist between sites, habitat differences should be minimized among individuals collected at any one site. Although micro-habitat differences cannot be eliminated—even in a test garden—the individuals at a given site have a much more similar environment in most cases than individuals collected at different sites (Figs. 2–5). Given the assumption that within-site habitat differences are minimal, within-site collections should indicate the variation, primarily genetic, which is expressed at a given site. Thus the overall comparisons indicate the average differences between species while the within-site comparisons (Tables 4–10) indicate the extent to which these average differences between species hold under the relatively uniform conditions at a given site.

Overall comparisons (Table 3)

Epidermal papillosity.—Although no quantitative measurements were made, some qualitative differences in the configuration of the external surface of the epidermis as seen in cross section are readily apparent. The epidermis of *Opuntia leptocaulis* (Fig. 6) and *O. kleiniae* (Fig. 7) is strongly undulating to papillose. *Opuntia imbricata* (Fig. 8) has an epidermis which is typically gently undulating. The surface of *O. phaeacantha* (Fig. 10) and *O. lindheimeri* (Fig. 9) is gently undulating to flat. *Opuntia leptocaulis* and *O. kleiniae*, although not separable from each other by this character, are readily distinguishable from the other species. The epidermis of *O. imbricata* is at times nearly as flat as that of *O. phaeacantha* or *O. lindheimeri*. The latter two species are not separable on the basis of external surface features.

Cuticular thickness.—The three cholla species typically have thinner cuticles than the two prickly pear species. Species means range from 2 μ (*O. imbricata*) to 4 μ (*O. leptocaulis*) among the chollas and from 7 μ to 9 μ for the two prickly

TABLE 3. Overall species comparisons.

Character	Student's t test 5% level[a]	Species	Number of collections	Mean[b]	Standard deviation	Coefficient of variation[c]	Range of collection means
Cuticular thickness (μ)	X	*O. imbricata*	17	2	1	50	1–4
	XX	*O. kleiniae*	5	3	1	33	1–4
	X	*O. leptocaulis*	12	4	1	25	2–7
	X	*O. lindheimeri*	11	7	3	43	1–10
	X	*O. phaeacantha*	4	9	3	33	7–12
Stomatal length (μ)	X	*O. leptocaulis*	12	34	4	12	28–40
	X	*O. imbricata*	17	34	3	9	30–38
	X	*O. kleiniae*	5	40	4	10	31–42
	X	*O. lindheimeri*	11	51	4	8	43–56
	X	*O. phaeacantha*	4	52	4	8	49–57
Stomatal density per mm^2	X	*O. lindheimeri*	11	35.3	13.5	38	17.0–62.6
	X	*O. phaeacantha*	4	35.5	11.6	32	26.0–50.9
	X	*O. leptocaulis*	12	36.5	12.0	33	22.6–53.3
	XX	*O. kleiniae*	5	49.6	19.6	39	18.5–70.3
	X	*O. imbricata*	17	62.1	19.0	31	38.5–99.9
Stomatal index of Salisbury		*O. leptocaulis*	12	0.6	0.2	33	0.3–0.9
	X	*O. kleiniae*	5	0.9	0.3	33	0.4–1.2
	X	*O. imbricata*	17	1.0	0.3	30	0.4–1.8
	XX	*O. lindheimeri*	11	1.3	0.5	38	0.6–2.3
	X	*O. phaeacantha*	4	1.5	0.4	27	0.9–1.9

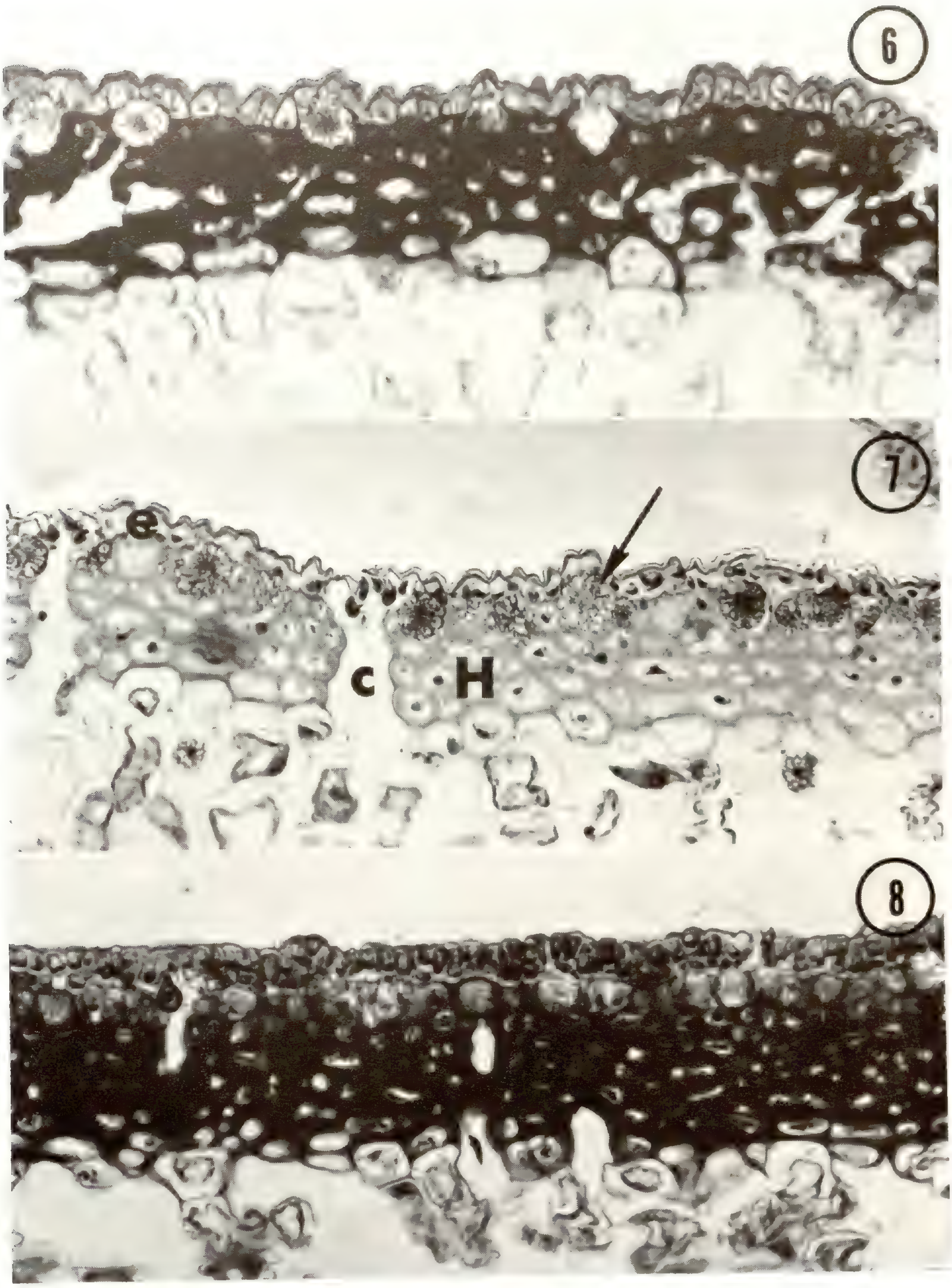
[a] Consecutive species with X's in the same column indicate those which are not significantly different at the 5% level.
[b] Computed from the collection means, not from the total number of observations for each species.
[c] The ratio of the standard deviation to the mean times 100.

TABLE 3. (Continued)

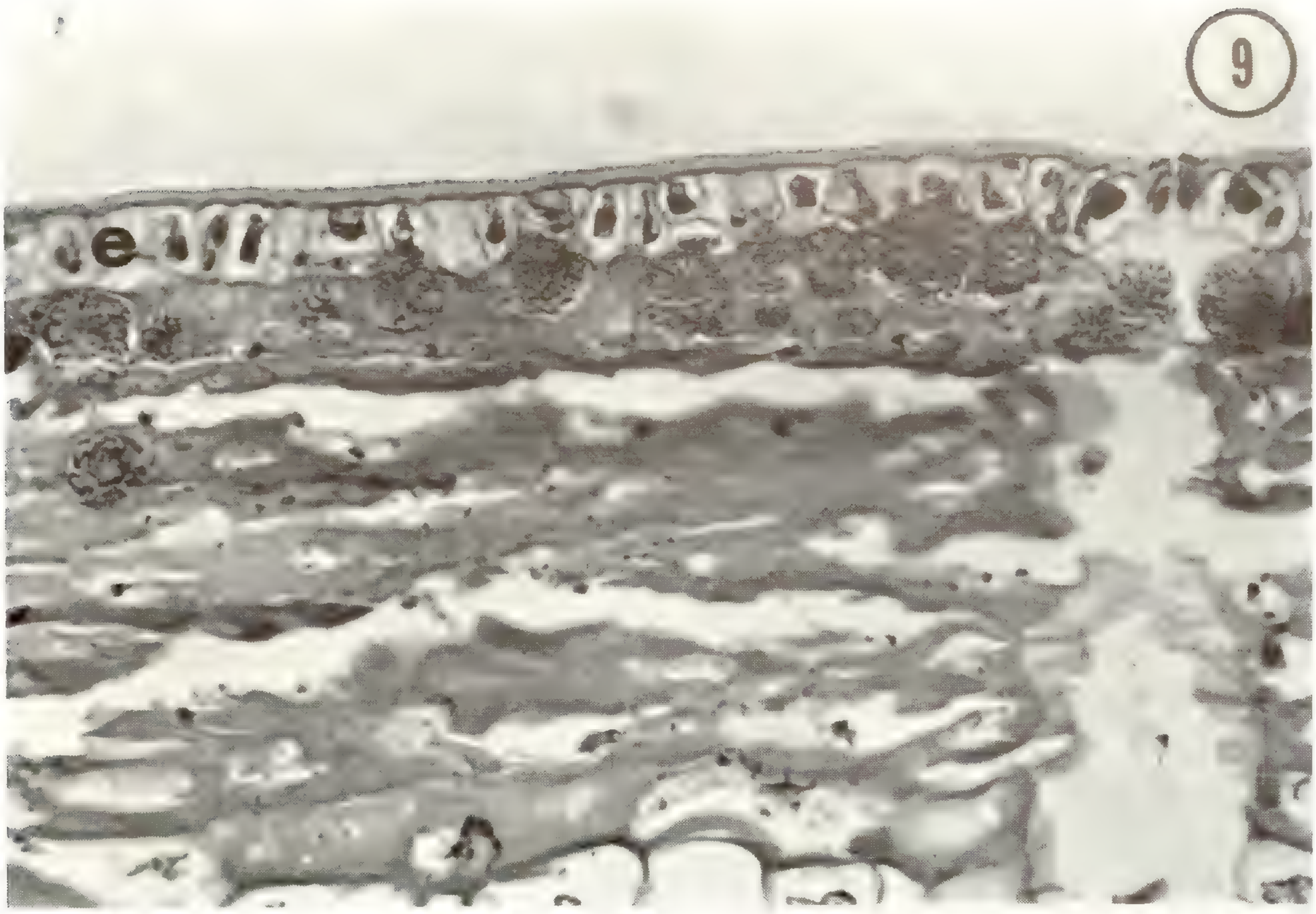
Character	Student's t test 5% level[a]		Species	Number of collections	Mean[b]	Standard deviation	Coefficient of variation[c]	Range of collection means
Hypodermal thickness (μ)		×	*O. kleiniae*	5	81	6	7	78–91
		×	*O. leptocaulis*	12	82	16	20	45–104
			O. imbricata	17	126	34	27	78–210
		×	*O. lindheimeri*	11	167	35	21	117–240
		×	*O. phaeacantha*	4	195	15	8	175–210
Vessel element length (μ)		×	*O. imbricata*	17	149	17	11	132–179
		××	*O. kleiniae*	5	154	23	15	120–175
		××	*O. leptocaulis*	12	169	14	8	145–191
		××	*O. phaeacantha*	4	182	23	13	147–200
		×	*O. lindheimeri*	11	187	24	13	138–216
Vessel element width (μ)			*O. leptocaulis*	12	20	2	10	16–22
			O. kleiniae	5	21	2	10	19–23
			O. imbricata	17	26	4	15	19–36
			O. phaeacantha	4	36	6	17	28–42
			O. lindheimeri	11	38	7	18	29–50
Length/width ratio			*O. lindheimeri*	11	5.0	1.2	24	3.8–7.5
			O. phaeacantha	4	5.2	1.3	25	4.3–7.2
			O. imbricata	17	5.7	0.7	12	4.9–7.4
			O. kleiniae	5	7.1	1.1	15	5.3–8.5
			O. leptocaulis	12	8.5	2.3	27	7.3–9.9

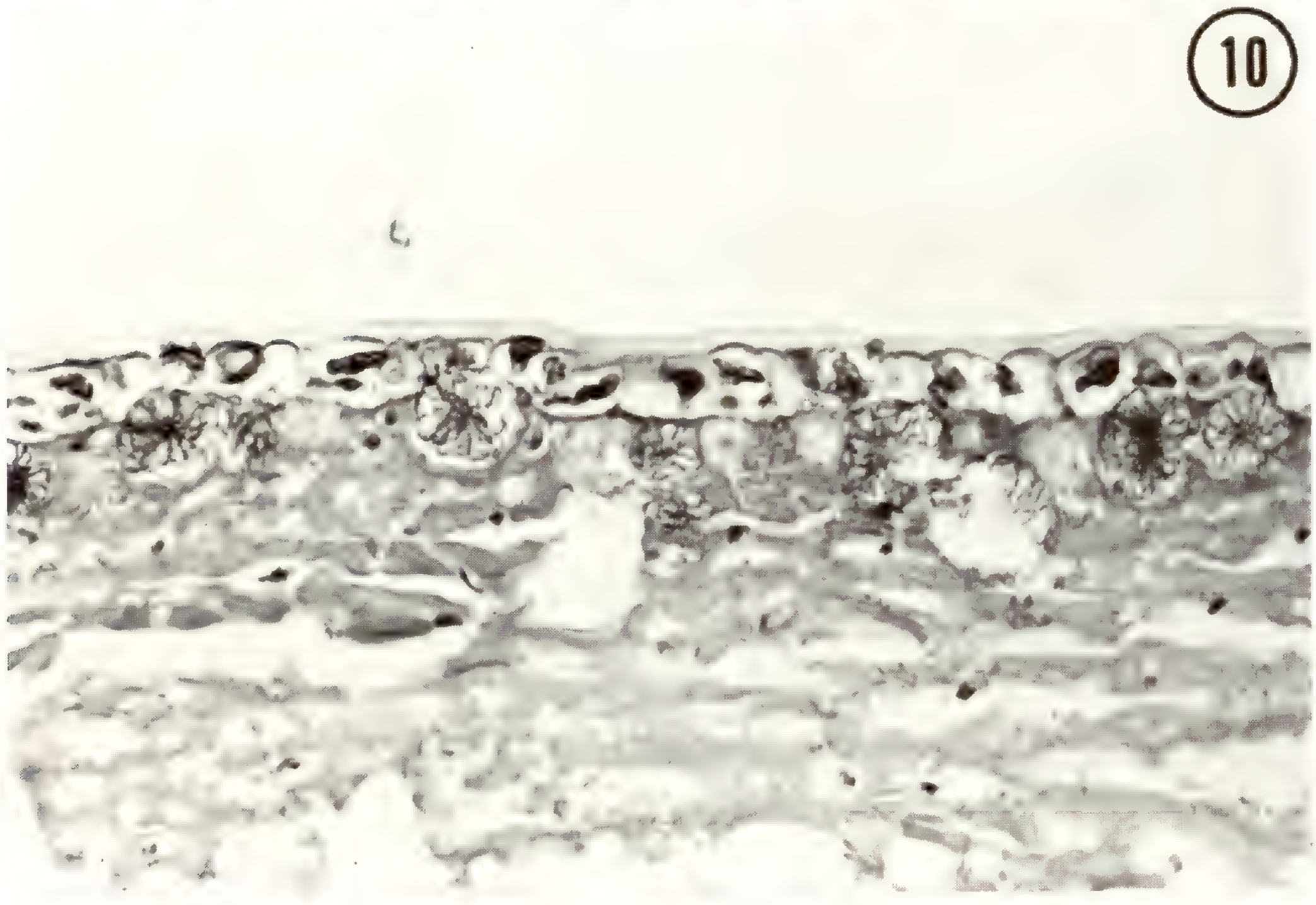
TABLE 3. (Continued)

Character	Student's t test 5% level[a]	Species	Number of collections	Mean[b]	Standard deviation	Coefficient of variation[c]	Range of collection means
Circumference/area ratio	×	*O. phaeacantha*	4	1.9	0.3	16	1.7–2.3
	×	*O. lindheimeri*	11	2.2	0.7	32	1.3–3.5
	×	*O. imbricata*	17	2.5	0.6	24	1.8–3.8
		O. kleiniae	5	4.4	0.7	16	3.4–5.0
		O. leptocaulis	12	7.3	1.5	21	5.2–10.0
Circumference (cm)		*O. leptocaulis*	12	1.7	0.4	24	1.3–2.5
		O. kleiniae	5	3.3	0.5	15	2.8–4.2
		O. imbricata	17	10.6	2.9	27	7.3–16.6
	×	*O. lindheimeri*	11	28.4	5.0	18	19.4–37.3
	×	*O. phaeacantha*	4	34.0	4.3	13	29.2–39.6
Area (cm^2)		*O. leptocaulis*	12	0.3	0.1	33	0.13–0.48
		O. kleiniae	5	0.8	0.3	37	0.61–1.23
		O. imbricata	17	4.4	1.9	43	1.90–9.20
	×	*O. lindheimeri*	11	13.8	6.2	34	5.50–25.60
	×	*O. phaeacantha*	4	17.5	3.7	21	12.20–20.10
Chromosome number ($2n$)		*O. imbricata*		22			
		O. kleiniae		44			
		O. leptocaulis		44			
		O. lindheimeri		66			
		O. phaeacantha		66			



FIGURES 6–8. Transverse sections of the epidermis (e) of *Opuntia* species. × 205.—6. *O. leptocaulis*.—7. *O. kleiniae*. The path of a substomatal canal (c) through the collenchymatous hypodermis (H) is shown. Druse crystals (arrow) comprising the subepidermal crystal layer are abundant.—8. *O. imbricata*.





FIGURES 9–10. Transverse sections of the epidermis (e) of *Opuntia* species. ×205.—9. *O. lindheimeri*.—10. *O. phaeacantha*.

pear species. Collection means range from 1 μ to 7 μ for the chollas and from 1 μ to 12 μ for the prickly pears.

Cuticular thickness is quite variable within each of the five species, coefficients of variation (standard deviation/mean × 100) ranging from 25% for *O. leptocaulis* to 50% for *O. imbricata*. Due to this amount of variation, species within a subgenus cannot, in most cases, be separated by the cuticular thickness. The two subgenera, however, are significantly different ($P < 0.05$) with respect to this character.

Stomatal length.—Stomatal length, *i.e.*, guard cell length, is less in the chollas than in the prickly pears (Figs. 11–15). Species means range from 34 μ (*O. leptocaulis*) to 40 μ (*O. kleiniae*) among the chollas and from 51 μ to 52 μ for the two prickly pear species. Collection means range from 28 μ to 42 μ for the chollas and from 43 μ to 57 μ for the prickly pears.

Stomatal length is quite constant in each species, the coefficients of variation ranging from 8 to 12% and averaging less than 10%. Stomatal length is also so consistent within each of the subgenera that none of the species in a subgenus are significantly different from one another. Differences between the subgenera are significant ($P < 0.05$).

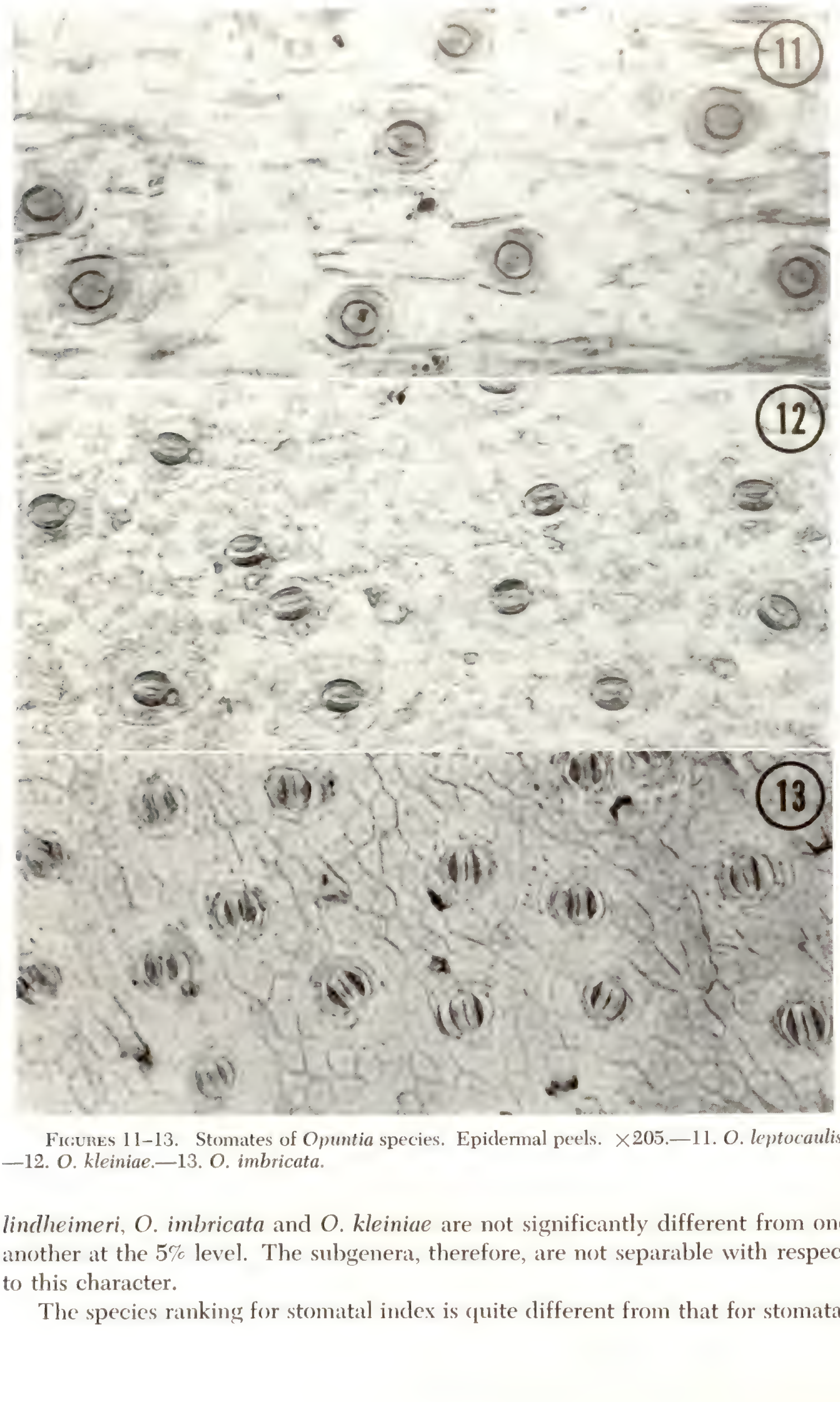
Stomatal density.—The two prickly pear species and the pencil cholla *O. leptocaulis* have the lowest stomatal densities, with species means ranging from 35.3 per mm^2 for *O. lindheimeri* to 36.5 per mm^2 for *O. leptocaulis*. Collection means for these three species all fall within the range recorded for *O. lindheimeri* (17.0–62.6). The other pencil cholla, *O. kleiniae*, had a similar range of collection means (18.5–70.3) but a somewhat higher species mean (49.6 per mm^2). *Opuntia imbricata*, the tree cholla, had the highest mean stomatal density (62.1 per mm^2) with a range of collection means from 38.5 to 99.9 stomates per mm^2.

Stomatal density is quite variable in each of the species, coefficients of variation ranging from 31% for *O. imbricata* to 39% for *O. kleiniae*. *Opuntia imbricata*, with the highest stomatal density, is significantly different ($P < 0.105$) from the three species with the lowest stomatal densities but no other species can be confidently separated at this level of significance. The two subgenera are, therefore, not separable with respect to this character.

Stomatal index.—The index used is that of Salisbury (1928), which is the ratio of stomatal density to stomatal density plus epidermal cell density times 100; $[s/(s + e) \times 100]$, *i.e.*, the percent of stomates as a function of the total number of epidermal cells.

The three chollas all have lower stomatal indices than those of the prickly pears, species means ranging from 0.6 for *O. leptocaulis* to 1.0 for *O. imbricata* and from 1.3 for *O. lindheimeri* to 1.5 for *O. phaeacantha*. Collection means show considerable overlap among the species, ranging from 0.3 (*O. leptocaulis*) to 1.8 (*O. imbricata*) among the chollas and from 0.6 to 2.3 (*O. lindheimeri*) among the prickly pears.

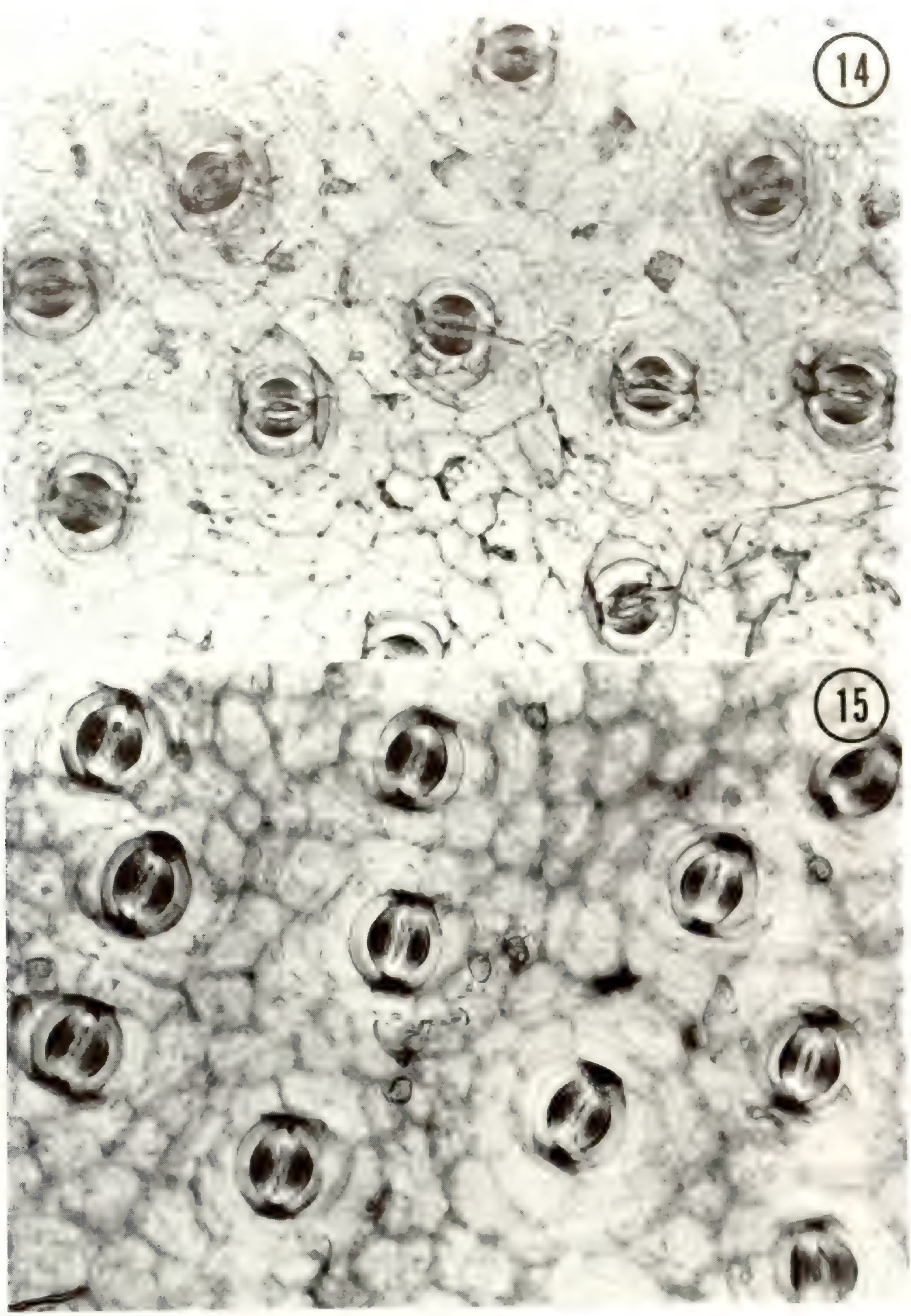
Stomatal index is roughly as variable as stomatal density within a species, coefficients of variation ranging from 27% (*O. phaeacantha*) to 38% (*O. lindheimeri*). While *O. leptocaulis* is significantly different from the other four species and *O. phaeacantha* is significantly different from the three chollas, *O.*



FIGURES 11–13. Stomates of *Opuntia* species. Epidermal peels. ×205.—11. *O. leptocaulis*. —12. *O. kleiniae*.—13. *O. imbricata*.

lindheimeri, *O. imbricata* and *O. kleiniae* are not significantly different from one another at the 5% level. The subgenera, therefore, are not separable with respect to this character.

The species ranking for stomatal index is quite different from that for stomatal



FIGURES 14–15. Stomates of *Opuntia* species. Epidermal peels. ×205.—14. *O. lindheimeri*.—15. *O. phaeacantha*.

density. For example, *O. leptocaulis*, which has approximately the same stomatal density as the two prickly pears, has a stomatal index which is quite different from that of the prickly pears. The differences in the species rankings for the two characters are due to differences in epidermal cell density.

Hypodermis.—The hypodermis consists of a single subepidermal layer of cells, many of which contain solitary druse crystals, and a band of strongly collenchymatous cells that is several layers thick (Fig. 19). The collenchymatous layers, the pseudo-hypodermis of Metcalf & Chalk (1950), are comprised of radially flattened, thick-walled cells with conspicuous intercellular pitting (Fig. 16). Bédélian (1911) observed that these layers reacted with phloroglucinol, an indication of the presence of lignin. In the present study, however, these cells did not stain with phloroglucinol or Sudan IV, which indicates the absence of both lignin and fatty substances. The collenchymatous layers form a compact band without intercellular spaces. The band is pierced at intervals by the substomatal canals, or more appropriately, tubes (Figs. 16, 18). These canals are frequently partially closed by the inward extensions of the subsidiary cells and/or the crystal-bearing hypodermal cells which protrude into the substomatal canal (Figs. 17–18).

The hypodermal thickness as measured here includes both the crystal-bearing layer and the collenchymatous layers. Since in all cases the crystal-bearing layer was only one cell thick, differences in hypodermal thickness are due primarily to differences in the thickness of the collenchymatous layers.

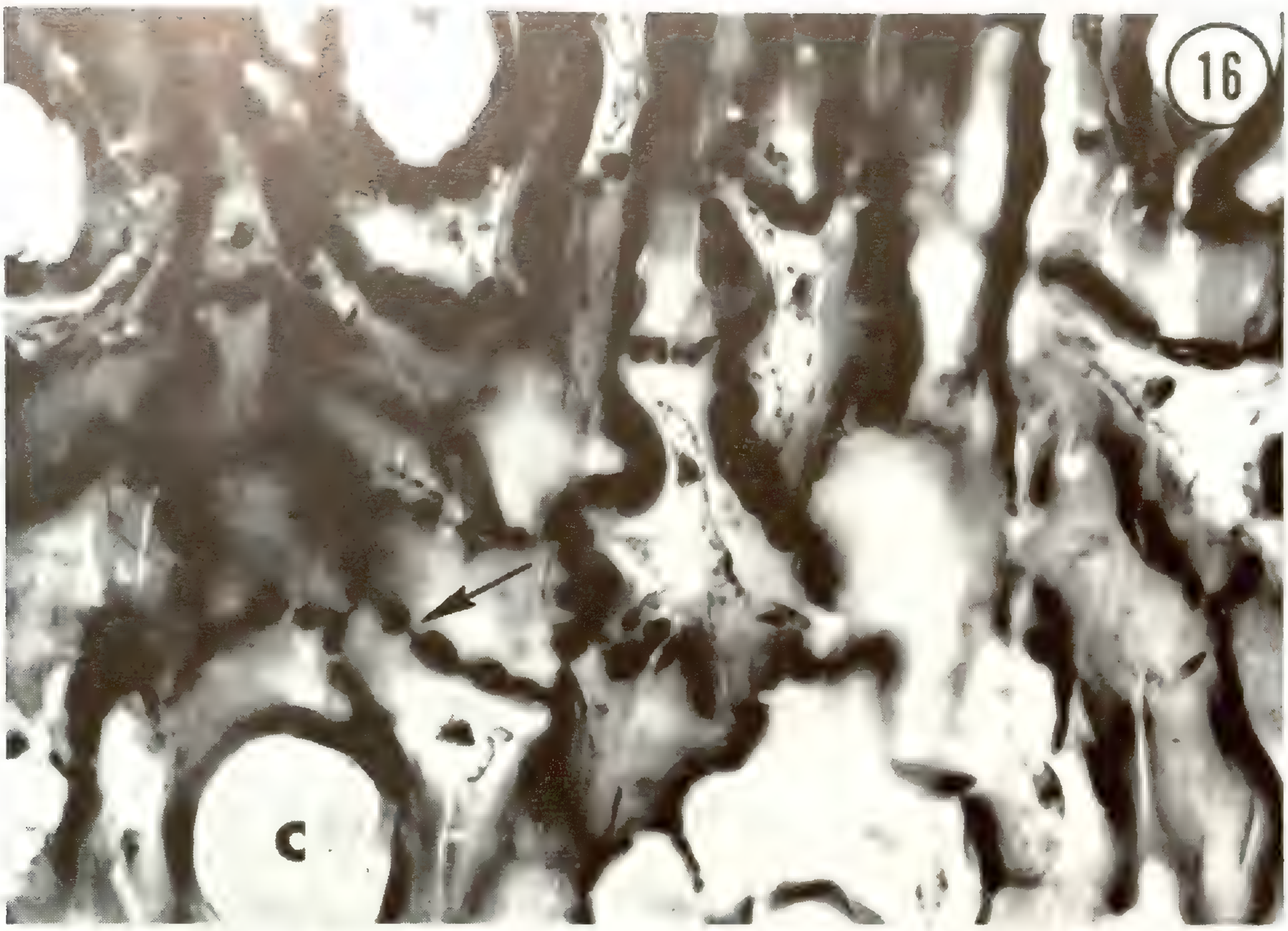
The two pencil chollas, *O. kleiniae* and *O. leptocaulis*, have the thinnest hypodermes, 81 μ and 82 μ respectively. The tree cholla, *O. imbricata*, has a thicker hypodermis (126 μ). The two prickly pear species, *O. lindheimeri* and *O. phaeacantha*, have hypodermes which are 167 μ and 195 μ thick.

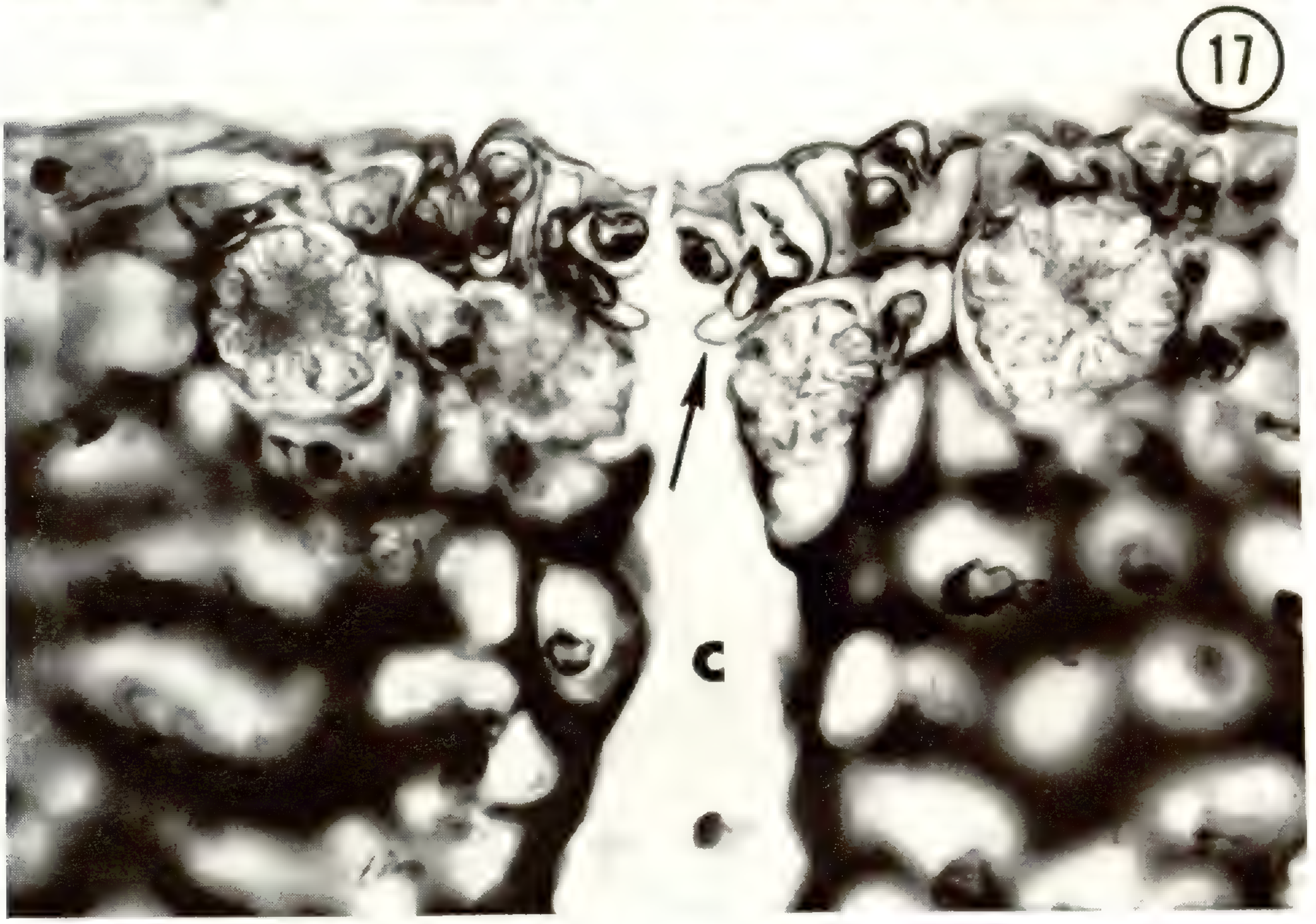
Collection means of hypodermal thickness show considerable overlap, 45 μ–104 μ for the pencil chollas, 78 μ–210 μ for the tree cholla, and 117 μ–240 μ for the prickly pears.

Hypodermal thickness is, on the whole, fairly constant within a species, coefficients of variation ranging from 7% for *O. kleiniae* to 27% for *O. imbricata* and averaging about 16% for the five species. Although members of morphologically similar pairs of species such as the two pencil chollas or the two prickly pears are not significantly different with respect to hypodermal thickness, the three different morphological forms represented by the pencil chollas, the tree cholla, and the prickly pears are each significantly different from each other. Thus the two subgenera are distinguishable on the basis of this character.

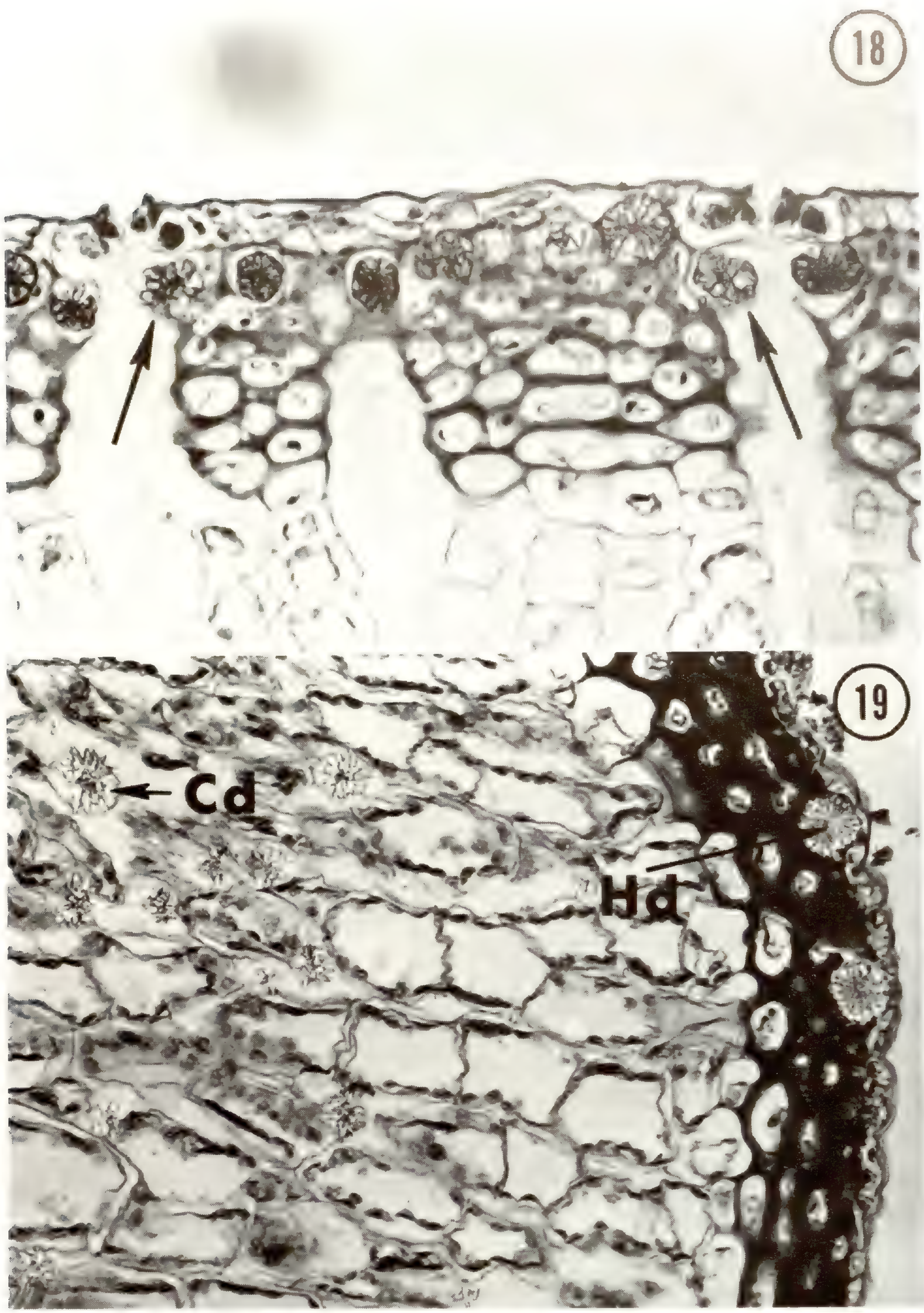
Mucilage cells.—Large, more or less spherical cells filled with a mucilaginous substance are found in abundance in the pith and cortex of all five species (Fig. 20). The number and distribution of these cells was not studied quantitatively.

Barrel tracheids.—These cells (Fig. 21) are "in shape midway between that of a barrel and that of a spindle; they are provided with locular or spiral thickening ridges, which are inserted on the thin wall by their narrow edge, and project far into the cell lumen. Generally these tracheids are also distinguished from the actual vessels by lack of perforation" (Metcalf & Chalk, 1950). Although these





FIGURES 16–17. Anatomical details of the stems of *Opuntia* species.—16. Intercellular pitting (arrow) in the collenchymatous hypodermis of *O. leptocaulis*, paradermal section. The substomatal canals (c) are circular to oval in transverse section. ×410.—17. Extension of subsidiary cells (arrow) into the substomatal canal (c) of *O. imbricata*. ×610.



FIGURES 18–19. Anatomical details of the stems of *Opuntia* species.—18. Extension of crystal-bearing cells (arrow) into the substomatal canals of *O. lindheimeri*. ×250.—19. Hypodermal (Hd) and cortical druses (Cd) in *O. leptocaulis*. ×220.

cells were reported by Schleiden (1845) to be absent from species of the subgenus *Opuntia*, they are abundant in all five species of the present study. Masses of these cells frequently occur associated with bundles and are always internal to them (Fig. 22). A single mass of barrel tracheids may sometimes appear to be associated with more than one bundle (Fig. 23). Schleiden indicated that the degree of association with the bundles may vary, in some cases not at all apparent while in other cases the barrel tracheids are an integral part of the bundle.

Vessel members.—Vessel members are simple perforate, small, and have opposite to alternate intervascular pitting. End walls are typically oblique and short tails are common (Figs. 24–28).

Vessel member length.—The vessel members are short. Of a sample of 600 species of dicotyledons, Metcalf & Chalk (1950) reported only 5% with a mean vessel member length of less than 200 μ. All five species in this study had mean vessel member lengths of under 200 μ. The chollas have the shortest mean vessel member lengths, ranging from 149 μ (*O. imbricata*) to 169 μ (*O. leptocaulis*). Mean vessel member lengths for the prickly pears are 182 μ and 187 μ for *O. phaeacantha* and *O. lindheimeri* respectively.

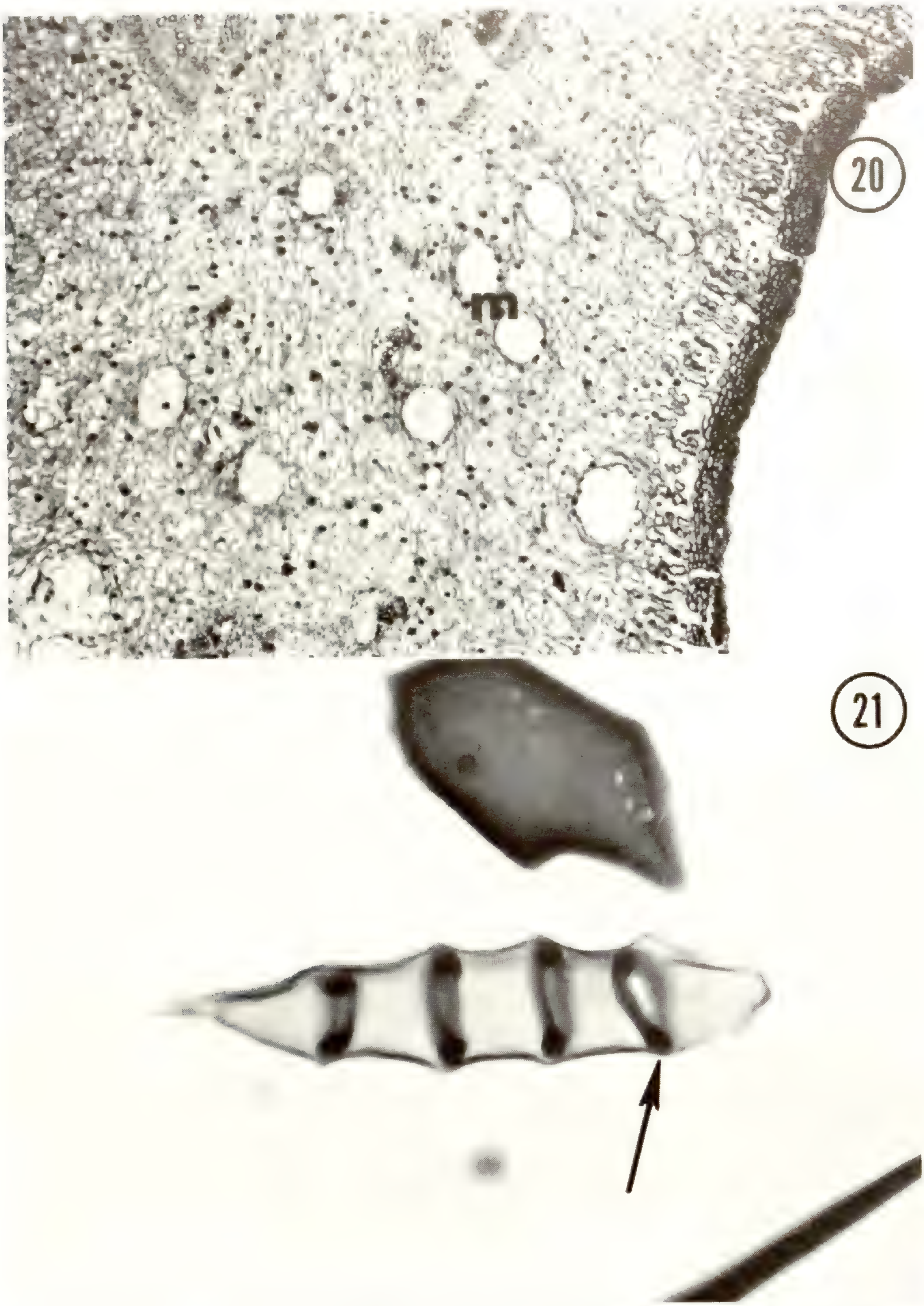
Collection means show a considerable overlap among the species, ranging in the chollas from 120 μ (*O. kleiniae*) to 191 μ (*O. leptocaulis*) and in the prickly pears from 138 μ to 216 μ (*O. lindheimeri*).

Length within each of the five species is relatively constant, coefficients of variation ranging from 8% (*O. leptocaulis*) to 15% (*O. kleiniae*) and averaging about 12%. There are, however, only rather small differences in length among the species, with the result that no two species which are ranked next to each other are significantly different at the 5% level. Thus neither subgenera nor morphological forms can consistently be distinguished on the basis of vessel member length.

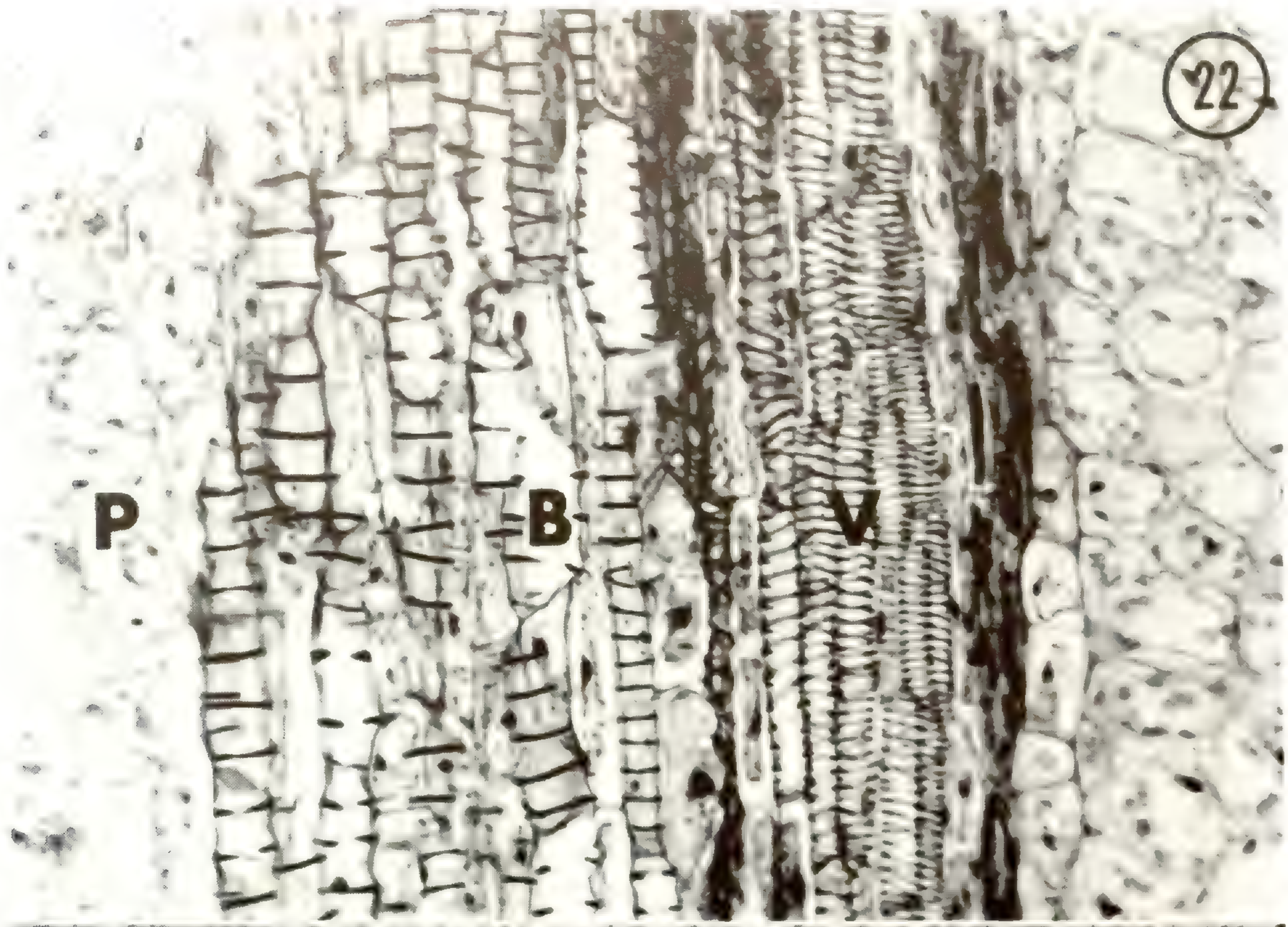
Vessel member width.—The vessels are narrow. Of 1500 species tabulated by Metcalf & Chalk (1950), only 10% had mean vessel widths of less than 40 μ. All five species in this study had mean vessel widths of less than 40 μ. The two pencil chollas, *O. leptocaulis* and *O. kleiniae*, have the narrowest vessels, 20 μ and 21 μ respectively. The tree cholla, *O. imbricata*, has wider vessels (26 μ), while the two prickly pears, *O. lindheimeri* and *O. phaeacantha*, have the widest vessels at 36 μ and 38 μ respectively.

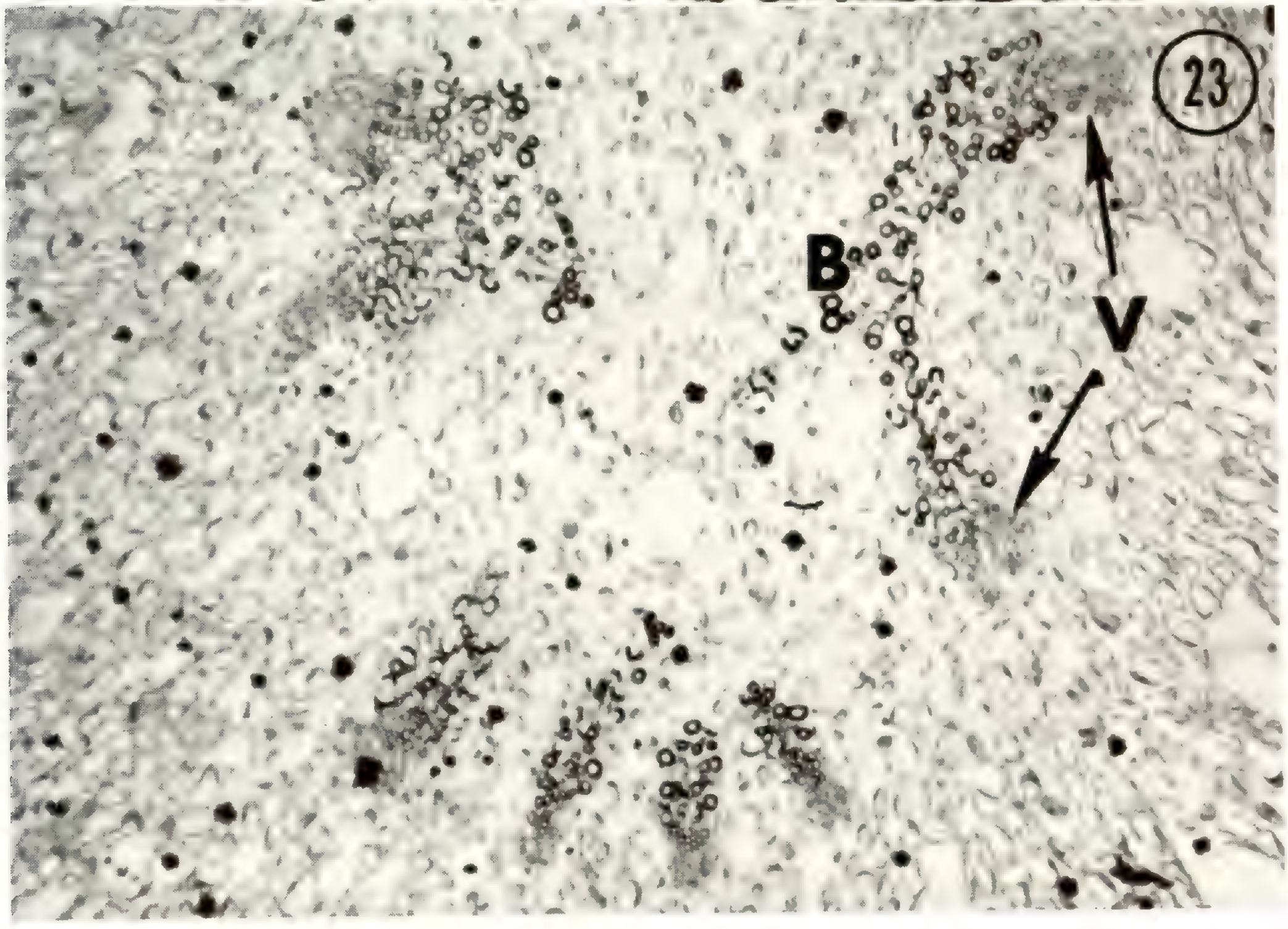
Collection means show quite a bit of overlap, ranging from 16 μ to 23 μ for the pencil chollas, 19 μ to 36 μ for the tree cholla, and 28 μ to 50 μ for the prickly pears.

Vessel width is approximately as variable as vessel element length in the five species, coefficients of variation averaging about 13% and ranging from 10% (*O. kleiniae*) to 18% (*O. lindheimeri*). Differences between species, however, are in some cases proportionately larger than was the case with vessel element length. Although species of the same growth form, *e.g.*, the two pencil cholla species, are not significantly different at the 5% level, the three different growth forms are each significantly different. The subgenera are therefore distinguishable on the basis of this character.



FIGURES 20–21. Anatomical details of the stems of *Opuntia kleiniae*.—20. Mucilage cavities (m) in the cortex. ×40.—21. Isolated barrel tracheid in a maceration. The rings of secondary wall are visible (arrow). ×640.

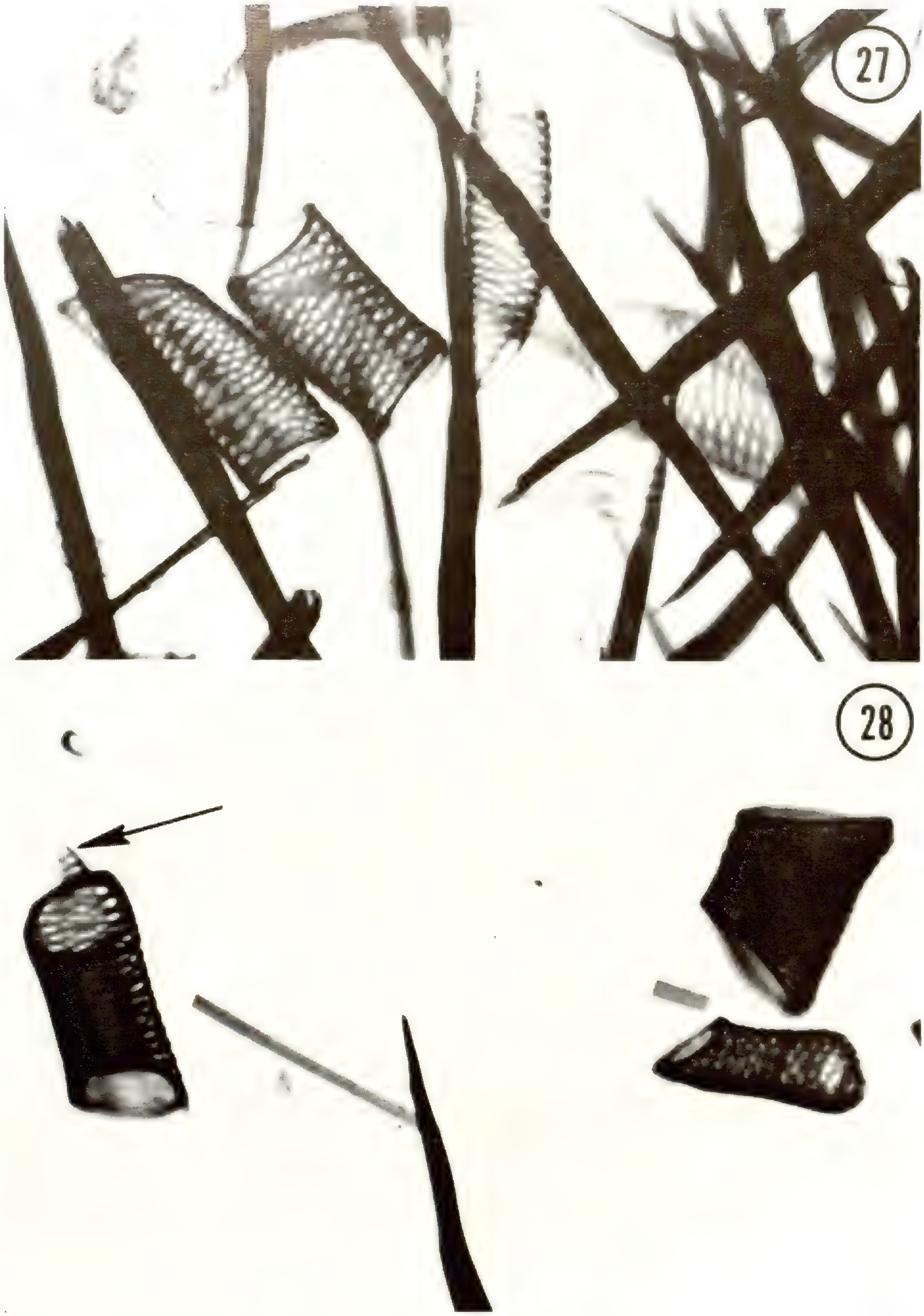




FIGURES 22–23. Association of barrel tracheids (B) with vascular bundles (V) in *Opuntia* species.—22. *O. leptocaulis*, longitudinal section. The barrel tracheids are located on the pith side (P) of the vascular bundle. ×200.—23. *O. imbricata*, transverse section. ×55.

FIGURES 24–26. Vessel members in macerations of *Opuntia* species.—24. *O. leptocaulis*. ×205.—25. *O. kleiniae*. Arrow indicates a short tail. ×205.—26. *O. imbricata*. ×205.

Vessel element length/width (l/w) ratio.—The pencil chollas have the largest vessel element l/w ratios, with species means of 8.5 and 7.1 for *O. leptocaulis* and *O. kleiniae*. *Opuntia imbricata* has a lower ratio (5.7) and *O. phaeacantha* (5.2) and *O. lindheimeri* (5.0) have the lowest ratios. Collection means show quite a



FIGURES 27–28. Vessel members in macerations of *Opuntia* species.—27. *O. lindheimeri*. ×205.—28. *O. phaeacantha*. Arrow indicates a short tail. ×205.

bit of overlap, ranging from 3.8 to 7.2 for the prickly pears, 4.9 to 7.4 for the tree cholla, and 5.3 to 9.9 for the pencil chollas.

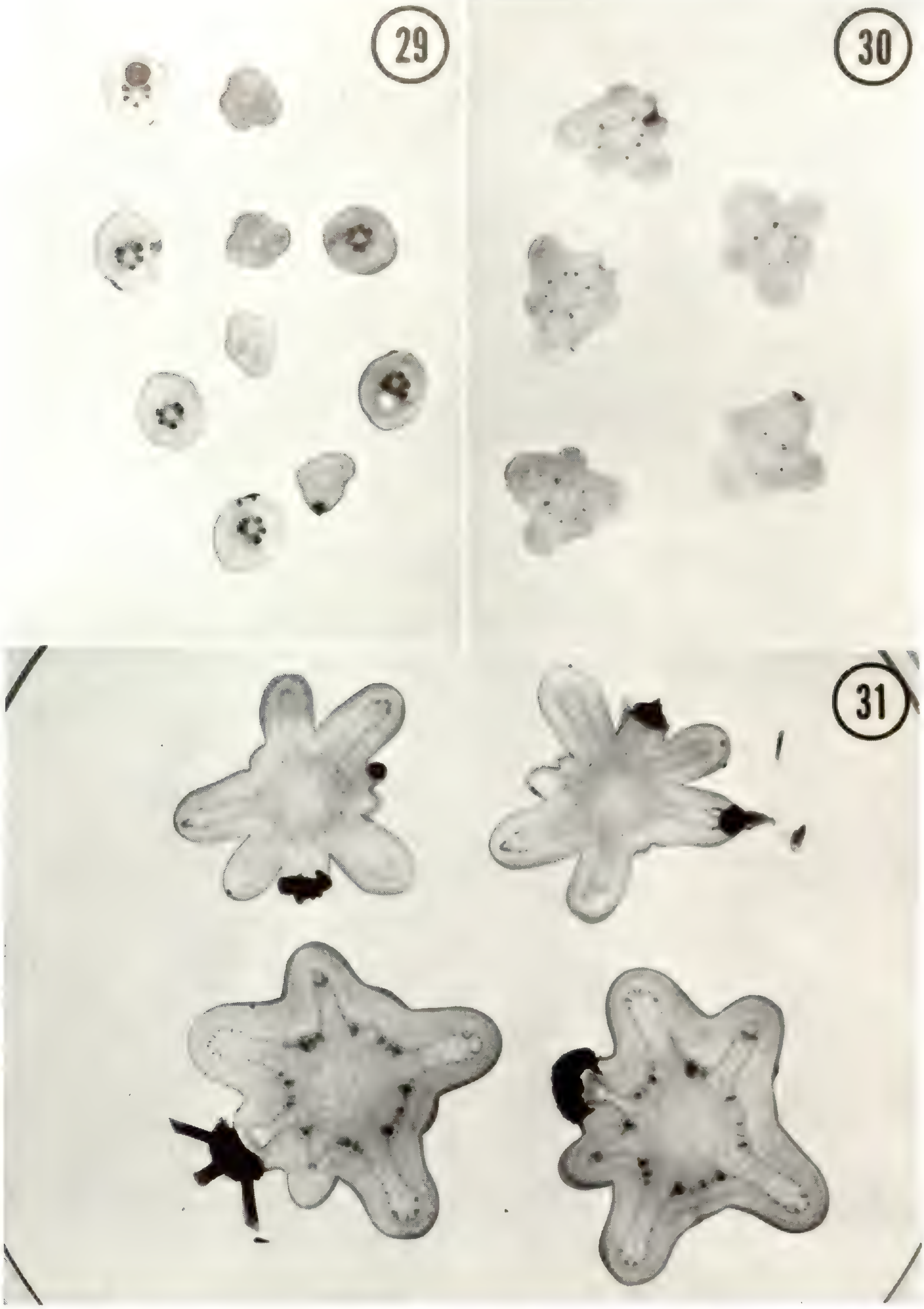
The ratios are typically more variable within a species than either length or width alone, coefficients of variation ranging from 12% (*O. imbricata*) to 27% (*O. leptocaulis*) and averaging nearly 21%.

The two pencil chollas are significantly different from the remaining three species but the two prickly pears are not distinguishable from the tree cholla. The subgenera therefore cannot be separated on the basis of vessel element l/w ratios.

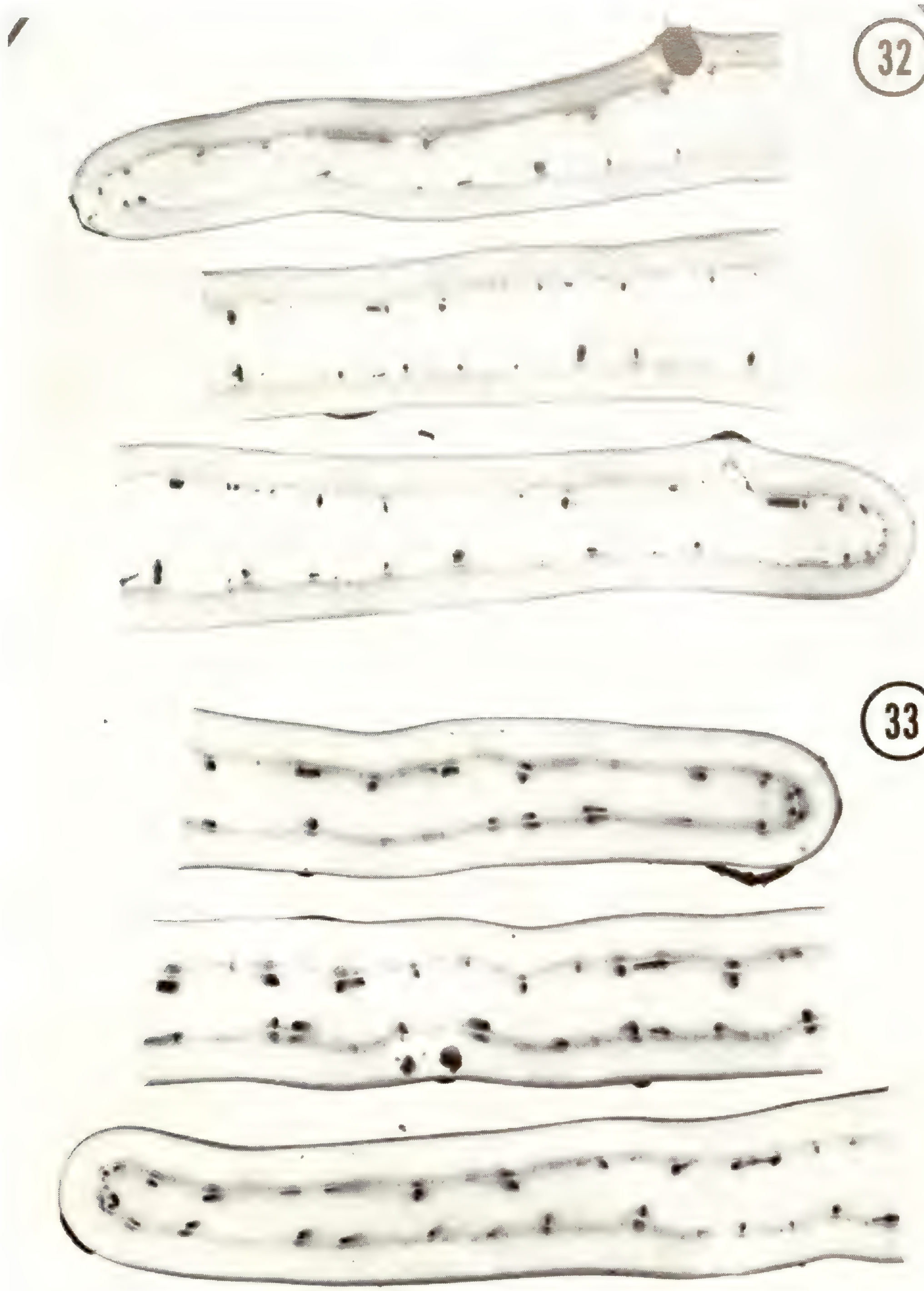
Circumference/area (c/a) ratio.—Several ways to determine the degree of succulence of plants have been suggested in the past. Delf (1912) preferred to use water content per unit surface of plant. This method is probably an accurate measure of succulence, particularly if the saturated weight rather than the fresh weight is used to determine the water content per unit surface. This method is not always practicable with all plant materials or in the field. Thoday (1931) stated that "the reciprocal of surface per unit weight is a rough measure of succulence." For many plants weight or volume would probably be equally satisfactory. If the reciprocal is not taken, the ratio of surface to weight (or volume) will be inversely proportional to the succulence, *i.e.*, a succulent plant will have a small external surface per unit of volume (or weight), and thus a low surface to volume ratio. Similarly, a non-succulent plant will have a large amount of surface per unit volume and thus a high surface to volume ratio. Since the circumference and area of a cross section of a cylindrical stem differ from the surface area and volume of that stem only by the height of the stem, a c/a ratio should also indicate the relative succulence of such plants, *i.e.*, a succulent plant will have a small circumference per unit of cross-sectional area and thus a low c/a ratio. Similarly, a non-succulent plant will have a large amount of circumference per unit of cross-sectional area and thus a high c/a ratio. For a piece of stem of a given height, the c/a ratio will equal the surface to volume ratio only if the stem is uniform from top to bottom. While this is seldom true, the c/a ratio should serve as a useful approximation of the surface to volume ratio.

This approximation should be reasonably good for the chollas since they are comprised of more or less fluted cylinders (Figs. 29–31). The approximation is not as good for the prickly pears whose stem segments (pads) are not uniform from the top to the bottom of the pad. The cross section of a pad is an ellipse (Figs. 32–33), the cross-sectional area of which is greater for sections made near the middle of the pad and less for sections made towards the top or bottom of the pad. As the area of sections towards the top or bottom of a pad decreases, the circumference will also decrease, but at a slower rate, since area is an exponential function while circumference is a linear function. The c/a ratio will therefore tend to increase, *i.e.*, indicate less succulence, towards the ends of the pad. The c/a ratios in Table 3 for *O. phaeacantha* and *O. lindheimeri* are based on sections taken near the middle of the pads and are therefore probably low, *i.e.*, the succulence of the prickly pears is somewhat exaggerated.

The c/a ratios for the pencil chollas are considerably higher than those of the



FIGURES 29–31. Transverse sections of stems of *Opuntia* species. In each figure the darkly stained vascular bundles which make up the vascular cylinder are visible. ×1.7.—29. *O. leptocaulis*.—30. *O. kleiniae*.—31. *O. imbricata*.



FIGURES 32–33. Transverse sections, in three parts, of stems of *Opuntia* species. In each figure the vascular bundles are visible. ×1.7.—32. *O. lindheimeri*.—33. *O. phaeacantha*.

other species. *Opuntia leptocaulis* and *O. kleiniae* have ratios of 7.3 and 4.4 respectively while the tree cholla has a c/a ratio of 2.5 and the two prickly pears have ratios of 2.2 (*O. lindheimeri*) and 1.9 (*O. phaeacantha*). There is considerable overlap of collection means among the latter three species, with means ranging from 1.3 to 3.5 in *O. lindheimeri* and from 1.8 to 3.8 in *O. imbricata*. *Opuntia kleiniae*, with collection means ranging from 3.4 to 5.0, overlaps only slightly with these three species. *Opuntia leptocaulis*, with collection means ranging from 5.2 to 10.0, does not overlap with any of the other species.

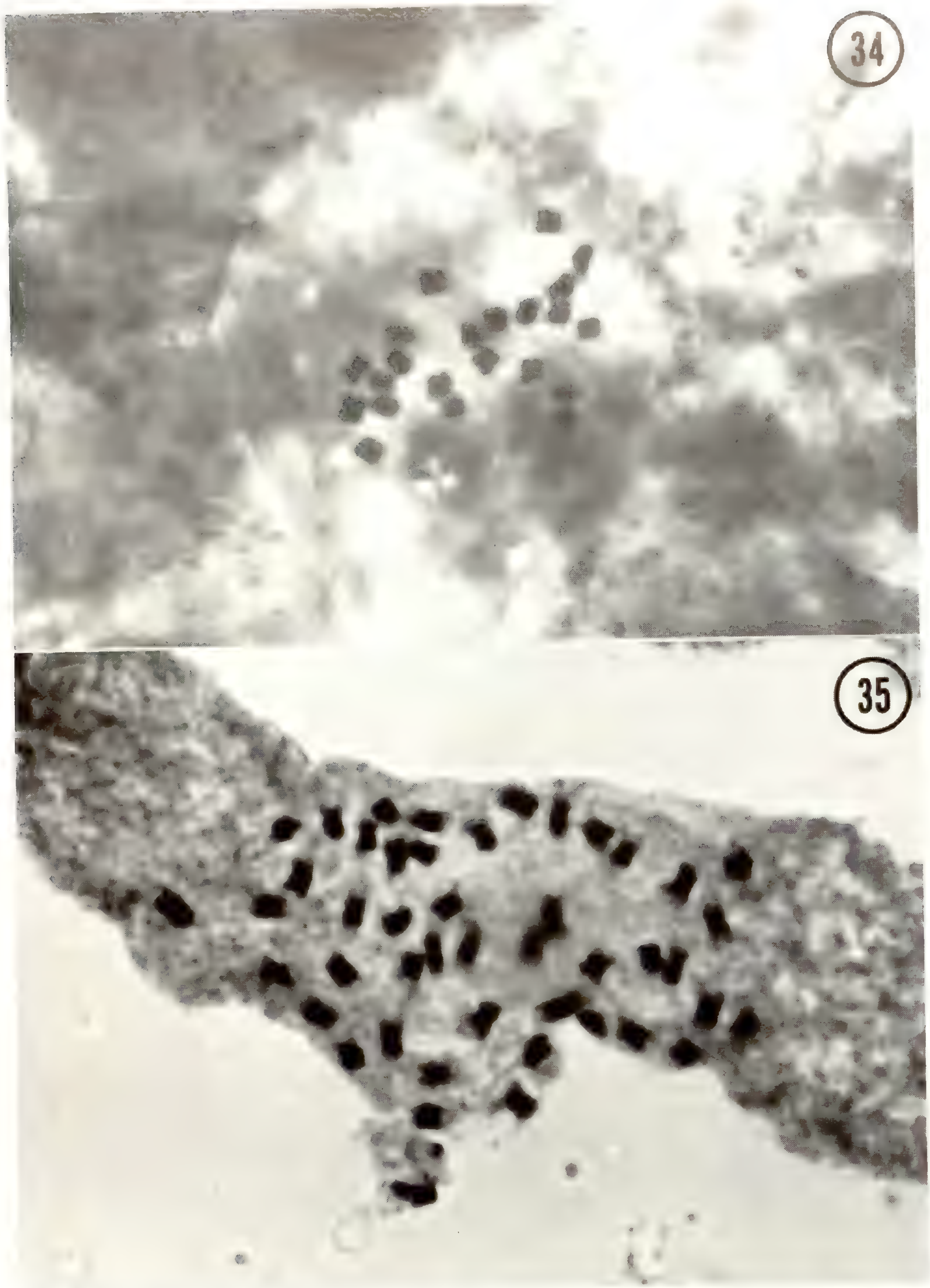
The c/a ratios are rather variable within a species, coefficients of variation ranging from 16% (*O. phaeacantha*) to 32% (*O. lindheimeri*) and averaging about 21%. The two pencil chollas are distinctly different from each other and from the other three species. The prickly pears and the tree cholla are not significantly different from one another at the 5% level, particularly when one considers that the values for the prickly pears are somewhat low. The two subgenera are therefore not different with respect to this character. It is unlikely, however, that the values for the prickly pears would be changed sufficiently by a more accurate estimate of surface area and volume to approach the values for the pencil chollas. The separation of the pencil chollas from the remaining species is considered to be a significant difference.

Circumference and area.—The circumference and area values are included in Table 3 primarily to provide an idea of the relative sizes of the various species. The mean circumference ranges from 1.7 cm for the pencil chollas to 34 cm for the prickly pears while the mean cross-sectional area ranges from 0.3 cm^2 for the pencil chollas to 17.5 cm^2 for the prickly pears.

Chromosome number.—The base number in *Opuntia* is $n = 11$ (Darlington & Wylie, 1955). A count of $2n = 22$ was obtained for the previously unreported *O. imbricata* (Fig. 34). A $2n$ number of 44 is reported for *Opuntia leptocaulis* by Fischer (1962) which is in agreement with the counts made in the present study (Fig. 35). *Opuntia kleiniae* from the geographic range covered by the present study is also reported by Fischer as $2n = 44$ although he reports counts of $2n = 22$ for *O. kleiniae* from Arizona. *Opuntia phaeacantha* has been reported as $2n = 66$ (Stockwell, 1935; Pinkava & McLeod, 1971). An approximate count of $2n = 66$ was made for the previously unreported *O. lindheimeri*, which is in agreement with a prediction by Dr. D. J. Pinkava (personal communication). Thus the tree cholla is diploid, the two pencil chollas are tetraploids, and the two prickly pears are hexaploids.

WITHIN-SITE COMPARISONS

The results for seven of the 21 collection sites (1, 3, 4, 8, 10, 14, 18) are summarized in Tables 4–10. Representatives of all three morphological types—pencil cholla, tree cholla, and prickly pear—were present at six of these seven sites. In four instances, twice at site 1 and once each at sites 4 and 18, collections were made of two individuals of a given species. These collections, termed here 'paired collections', involved *Opuntia lindheimeri* on two occasions and *O. imbricata* and *O. leptocaulis* on the remaining two occasions. If the values of a given character



FIGURES 34–35. Chromosomes of *Opuntia* species. ×2400.—34. *O. imbricata* ($2n = 22$). —35. *O. leptocaulis* ($2n = 44$).

TABLE 4. Within-site comparisons. Site 1.

	O. leptocaulis	*O. leptocaulis*	*O. lindheimeri*	*O. lindheimeri*
Cuticular thickness (μ)	5 (+)[a]	2 (−−)	7	9 (+)
Stomatal length (μ)	40 (++)[b]	28 (−−)	55 (+)	50 (−)
Stomatal density/mm^2	30.0 (−)	43.6 (+)	17.0 (−−)	27.0 (−)
Stomatal index	0.5 (−)	0.5 (−)	0.7 (−−)	0.6 (−−)
Hypodermal thickness (μ)	91 (+)	91 (+)	200 (+)	130 (−−)
Vessel element length (μ)	175 (+)	171 (+)	193 (+)	195 (+)
Vessel element width (μ)	22 (+)	21 (+)	50 (++)	49 (++)
Length/width ratio	7.9 (−)	8.1 (−)	3.9 (−)	4.0 (−)
Circumference/area ratio	7.3[c]	10.0 (++)	2.3 (+)	3.1 (++)
Circumference (cm)	1.9 (+)	1.3 (−)	28.8 (+)	27.8 (−)
Area (cm^2)	0.26 (−)	0.13 (−−)	12.5 (−)	8.9 (−)

[a] Single sign indicates the value is above (+) or below (−) the species mean for that character (see Table 3).
[b] Double sign indicates the value is more than one standard deviation above (++) or below (−−) the species mean for that character (see Table 3).
[c] Absence of sign indicates the value coincides with the species mean for that character (see Table 3).

differ by more than one standard deviation, the two members are considered here to be markedly different for that characteristic.

Cuticular thickness.—At three of the seven sites (Tables 4, 9, 10), the species fall in the same relative positions according to cuticular thickness as they do in the overall comparisons (Table 3). If the relative positions of species which are not significantly different from one another at the 5% level in the overall comparisons are disregarded, site 10 (Table 8) also is in agreement with the rankings of the overall comparisons. Cuticular thickness was markedly different between members of two of the four paired collections (*O. leptocaulis*, Table 4; *O. imbricata*, Table 6). At site 3 (Table 5), the values for all collections were below the average values for their respective species.

Stomatal length.—At two of the seven sites (Tables 4, 7), the species fall in the same relative positions according to stomatal length as they do in the overall comparisons (Table 3). If the relative positions of species which are not significantly different from one another at the 5% level are disregarded, all seven sites are in agreement with the overall comparisons, *i.e.*, the stomates of the

TABLE 5. Within-site comparisons. Site 3. For explanation of symbols see Table 4.

	O. leptocaulis	*O. imbricata*	*O. lindheimeri*
Cuticular thickness (μ)	3 (−)	1 (−)	3 (−−)
Stomatal length (μ)	33 (−)	33 (−)	48 (−)
Stomatal density/mm^2	41.5 (+)	38.6 (−−)	28.6 (−)
Stomatal index	0.9 (++)	0.6 (−−)	1.5 (+)
Hypodermal thickness (μ)	91 (+)	145 (+)	155 (−)
Vessel element length (μ)	191 (++)	154 (+)	158 (−−)
Vessel element width (μ)	22 (+)	25 (−)	38
Length/width ratio	8.7 (+)	6.3 (+)	4.1 (−)
Circumference/area ratio	7.5 (+)	2.2 (−)	2.1 (−)
Circumference (cm)	1.5 (−)	7.7 (−)	23.2 (−−)
Area (cm^2)	0.20 (−)	3.5 (−)	10.7 (−)

TABLE 6. Within-site comparisons. Site 4. For explanation of symbols see Table 4.

	O. leptocaulis	*O. imbricata*	*O. imbricata*	*O. lindheimeri*
Cuticular thickness (μ)	4	1 (−)	3 (+)	4 (−)
Stomatal length (μ)	33 (−)	36 (+)	29 (−−)	52 (+)
Stomatal density/mm^2	53.0 (++)	62.0 (−)	71.6 (+)	42.9 (+)
Stomatal index	0.8 (+)	1.2 (+)	1.1 (+)	2.3 (++)
Hypodermal thickness (μ)	91 (+)	117 (−)	145 (+)	170 (+)
Vessel element length (μ)	161 (−)	141 (−)	179 (++)	216 (++)
Vessel element width (μ)	20	28 (+)	36 (++)	29 (−−)
Length/width ratio	7.9 (−)	5.1 (−)	4.9 (−−)	7.6 (++)
Circumference/area ratio	5.2 (−−)	2.0 (−)	2.3 (−)	3.5 (++)
Circumference (cm)	2.5 (++)	8.3 (−)	8.6 (−)	19.4 (−−)
Area (cm^2)	0.48 (++)	4.1 (−)	3.6 (−)	5.5 (−−)

chollas are always smaller than those of the prickly pears. Stomatal length is markedly different between members of three of the four paired collections (*O. leptocaulis*, *O. lindheimeri*, Table 4; *O. imbricata*, Table 6). At site 3 (Table 5), the values for all collections are below the average values for their species.

Stomatal density.—At two of the seven sites (Tables 4, 8), the species fall in the same relative positions according to stomatal density as they do in the overall comparisons (Table 3). If the relative positions of species which are not significantly different from one another at the 5% level are disregarded, sites 8, 14 and 18 (Tables 7, 9, 10) are also in agreement with the rankings of the overall comparisons. Stomatal density is markedly different between members of one of the four paired collections (*O. leptocaulis*, Table 4). At site 14 (Table 9), the values for all collections are below the average values for their species.

Stomatal index.—At four of the seven sites (Tables 4–6, 8), the species fall in the same relative positions according to stomatal index as they do in the overall comparisons (Table 3). If the relative positions of species which are not significantly different from one another at the 5% level are disregarded, sites 8 and 18 (Tables 7, 10) are also in agreement with the rankings of the overall comparisons. Stomatal index is not markedly different between members of any of the four paired collections. At site 1 (Table 4), the values for all collections are below the average values for their species, while at site 4 (Table 6), the values for all collections are above the average value for their species.

Hypodermal thickness.—At five of the seven sites (Tables 4–6, 8–9), the species fall in the same relative positions according to hypodermal thickness as they do in the overall comparisons (Table 3). If the relative positions of species which are not significantly different from one another at the 5% level are disregarded, this number does not change. Hypodermal thickness is markedly different between members of two of the four paired collections (*O. lindheimeri*, Tables 4, 10). At site 8 (Table 7), the values for all collections are below the average values for their species.

Vessel element length.—At two of the seven sites (Tables 4, 10), the species fall in the same relative position according to vessel element length as they do in the overall comparisons (Table 3). If the relative positions of species which are

TABLE 7. Within-site comparisons. Site 8. For explanation of symbols see Table 4.

	O. leptocaulis	*O. kleiniae*	*O. imbricata*	*O. lindheimeri*
Cuticular thickness (μ)	3 (–)	3	3 (+)	1 (––)
Stomatal length (μ)	31 (–)	41 (+)	36 (+)	47 (–)
Stomatal density/mm^2	53.3 (++)	70.3 (++)	58.6 (–)	31.2 (–)
Stomatal index	0.8 (+)	1.2 (+)	0.8 (–)	0.8 (–)
Hypodermal thickness (μ)	78 (–)	78 (–)	117 (–)	117 (––)
Vessel element length (μ)	184 (++)	170 (+)	157 (+)	173 (–)
Vessel element width (μ)	19 (–)	20 (–)	25 (–)	35 (–)
Length/width ratio	9.8 (+)	8.5 (++)	6.4 (+)	5.0
Circumference/area ratio	7.2 (–)	4.5 (+)	2.0 (–)	2.1 (–)
Circumference (cm)	1.8 (+)	2.8 (–)	13.1 (+)	26.6 (–)
Area (cm^2)	0.25 (–)	0.61 (–)	6.3 (+)	12.1 (–)

not significantly different from one another at the 5% level are disregarded, this number does not change. Vessel element length is markedly different between members of one of the four paired collections (*O. imbricata*, Table 6). At site 1 (Table 4), the values for all collections are above the average values for their species, while at site 10 (Table 8), the values for all collections are below the average values for their species.

Vessel width.—At six of the seven sites (Tables 4–5, 7–10), the species fall in the same relative positions according to vessel width as they do in the overall comparisons (Table 3). If the relative positions of species which are not significantly different from one another at the 5% level are disregarded, this number does not change. Vessel width is markedly different between members of one of the four paired collections (*O. imbricata*, Table 6). At site 1 (Table 4), the values for all collections are above the average values for their species, while at sites 8, 14, and 18 (Tables 7, 9–10), the values for all collections are below the average values for their species.

Vessel element length/width (l/w) ratio.—At six of the seven sites (Tables 4–5, 7–10), the species fall in the same relative positions according to l/w ratios as they do in the overall comparisons (Table 3). If the relative positions of species which are not significantly different from one another at the 5% level are ignored,

TABLE 8. Within-site comparisons. Site 10. For explanation of symbols see Table 4.

	O. kleiniae	*O. imbricata*	*O. lindheimeri*
Cuticular thickness (μ)	1 (––)	3 (+)	8 (+)
Stomatal length (μ)	34 (––)	37 (+)	43 (––)
Stomatal density/mm^2	61.5 (+)	44.3 (–)	62.6 (++)
Stomatal index	0.8 (–)	1.2 (+)	1.5 (+)
Hypodermal thickness (μ)	91 (+)	110 (–)	150 (–)
Vessel element length (μ)	138 (–)	135 (–)	138 (––)
Vessel element width (μ)	19 (–)	26	36 (–)
Length/width ratio	7.1	5.3 (–)	3.8 (–)
Circumference/area ratio	5.0 (+)	1.8 (––)	3.0 (++)
Circumference (cm)	3.1 (–)	16.6 (++)	26.5 (–)
Area (cm^2)	0.61 (–)	9.2 (++)	8.7 (–)

TABLE 9. Within-site comparisons. Site 14. For explanation of symbols see Table 4.

	O. leptocaulis	*O. imbricata*	*O. phaeacantha*
Cuticular thickness (μ)	3 (–)	2	12 (+)
Stomatal length (μ)	35 (+)	32 (–)	49 (–)
Stomatal density/mm^2	22.8 (––)	58.3 (–)	26.0 (–)
Stomatal index	0.4 (–)	1.3 (+)	0.9 (––)
Hypodermal thickness (μ)	78 (–)	135 (+)	195
Vessel element length (μ)	162 (–)	157 (+)	149 (––)
Vessel element width (μ)	16 (––)	25 (–)	35 (–)
Length/width ratio	9.9 (+)	6.2 (+)	4.3 (–)
Circumference/area ratio	10.0 (++)	2.6 (+)	2.3 (++)
Circumference (cm)	1.5 (–)	9.0 (–)	29.2 (––)
Area (cm^2)	0.15 (––)	3.4 (–)	12.2 (––)

site 4 (Table 6) is also in agreement with the rankings of the overall comparisons. Length/width ratios are not markedly different between members of any of the four paired collections. At site 1 (Table 4), the values for all collections are below the average values for their species.

Circumference/area (c/a) ratio.—At four of the seven sites (Tables 4–5, 9–10), the species fall in the same relative positions according to c/a ratios as they do in the overall comparisons (Table 3). If the relative positions of species which are not significantly different from one another at the 5% level are disregarded, all seven sites are in agreement with the rankings of the overall comparisons. Circumference/area ratios are markedly different between members of two of the four paired collections (*O. leptocaulis*, *O. lindheimeri*, Table 4). At site 14 (Table 9), the values for all collections are above the average values for their species.

Circumference.—At all seven sites, the species fall in the same relative positions according to circumference as they do in the overall comparisons (Table 3). Circumference is not markedly different between members of any of the four paired collections. At sites 3 and 14 (Tables 5, 9), the values for all collections are below the average values for their species.

Area.—At six of the seven sites (Tables 4–7, 9–10), the species fall in the same

TABLE 10. Within-site comparisons. Site 18. For explanation of symbols see Table 4.

	O. leptocaulis	*O. imbricata*	*O. lindheimeri*	*O. lindheimeri*
Cuticular thickness (μ)	4	3 (+)	10 (+)	8 (+)
Stomatal length (μ)	37 (+)	33 (–)	52 (+)	52 (+)
Stomatal density/mm^2	26.8 (–)	99.9 (++)	44.3 (+)	38.5 (+)
Stomatal index	0.5 (–)	1.8 (++)	1.6 (+)	1.4 (+)
Hypodermal thickness (μ)	65 (––)	210 (++)	240 (++)	170 (+)
Vessel element length (μ)	150 (––)	145 (–)	189 (+)	197 (+)
Vessel element width (μ)	19 (–)	19 (––)	34 (–)	31 (–)
Length/width ratio	8.0 (–)	7.5 (++)	5.5 (+)	6.3 (++)
Circumference/area ratio	6.8 (–)	3.5 (++)	2.0 (–)	2.2
Circumference (cm)	1.7	9.1 (–)	28.8 (+)	27.1 (–)
Area (cm^2)	0.25 (–)	2.6 (–)	14.2 (+)	12.3 (–)

TABLE 11. Correlation of characters.

Character	Character 2	3	4	5	6	7	Stomatal index
1. Vessel width	.7553	−.6185	.6725	.5519	.4367	−.2279[a]	.3066
2. Stomatal length		−.4906	.6197	.7558	.6173	−.4511	.4162
3. Circumference/area			−.6057	−.2129[a]	.0008[a]	−.1461[a]	−.4667
4. Hypodermal thickness				.5177	.3722	.1139[a]	.6479
5. Cuticular thickness					.4981	−.4102	.2294[a]
6. Vessel element length						−.3966	.2230[a]
7. Stomatal density							.4391

[a] Correlation coefficients with an absolute value less than .3000 indicate correlations which are not significant at the 5% level (Fisher & Yates, 1938).

relative positions according to area as they do in the overall comparisons (Table 3). If the relative positions of species which are not significantly different from one another at the 5% level are disregarded, this number does not change. Area is markedly different between members of one of the four paired collections (*O. leptocaulis*, Table 4). At sites 1, 3, and 14 (Tables 4–5, 9), the values for all collections are below the average values for their species.

CORRELATION OF CHARACTERS

The configuration of the external epidermal cell surface was not quantified and thus is not included in the calculations of character correlations. It appears, however, that the degree of papillosity or unevenness of the external epidermal surface is directly related to the circumference/area ratio and inversely related to hypodermal thickness and vessel width. For example, the pencil chollas, which have quite papillose epidermal cells, also have a high circumference/area ratio but have thin hypodermes and narrow vessels.

The correlations of all other characters studied is given in Table 11.

DISCUSSION

External epidermal surface.—Boosfeld (1920) reported that epidermal cells varied from smooth to papillose in the Cactaceae. It is evident from the illustrations in a paper by Bailey (1964*b*) that both papillose and smooth epidermal cells occur in the leaf-bearing Cactaceae. Anderson & Boke (1969), working with the cactus genus *Pelecyphora*, stated: "It is worth noting that at the specific level *P. aselliformis* and *Encephalocarpus strobiliformis* [now *P. strobiliformis*] may be distinguished by means of tubercle sections alone. Although sectioned specimens of both species are much alike in other respects, epidermal cells of *E. strobiliformis* are conspicuously papillose, those of *P. aselliformis* much less so." In the Juglandaceae as well, the external form of leaf epidermal cells seems to be consistent within taxa (D. E. Stone, unpublished). It is, therefore, apparent that the form of the external surface of the epidermal cells is rather constant within a taxon. This would imply that the epidermal morphology of a taxon has been fixed, either by selection or by chance, in forms ancestral to present day species or species groups.

With regard to the Opuntiae under study, the epidermal papillosity seems to be related to the stem form, since the two pencil chollas both have papillose epidermes and the two prickly pears both have smooth epidermes. The epidermal papillosity is not, however, related directly to the degree of curvature of the stem surface, since species with both curved and flat regions on their stems have a consistent type of epidermal surface.

Cuticle thickness.—It is clear that both environmental and genetic factors play a part in determining the thickness of the cuticle of the species in the present study. It is certain that genetic differences account for the difference in cuticular thickness seen between the pencil chollas and the prickly pears. At only one of the seven sites in the within-site comparisons, do the values for all collections fall above or below the average values for their respective species. If cuticle thickness is primarily under environmental control, more sites should show such a uniform deviation from species norms. A probable genetic influence on cuticular thickness is also seen in the two paired collections which have members that are quite different from one another with respect to cuticle thickness. At approximately half of the seven sites, the species fall in the same relative positions according to cuticle thickness as they do in the overall comparisons. This indicates the mutual influence of genetic and environmental factors since if either were considerably more important than the other, more sites would be expected to parallel the overall comparisons.

Some possible environmental effects on cuticular thickness in *Opuntia* may be seen by comparing the results of previous studies with those of the present study. Brown (1920), working with plants grown in nature, reported a cuticle thickness of 11 μ for *O. blakeana* (= *O. phaeacantha*) which agrees closely with the average cuticular thickness of 9 μ for *O. phaeacantha* in the present study. On the other hand, Bédélian (1911), working with cultivated plants, reported cuticle thicknesses of 1.44 μ and 0.72 μ for *O. leptocaulis* and *O. frutescens* (= *O. leptocaulis*) and 0.36 μ for *O. rosea* (= *O. imbricata*). These figures are all considerably smaller than those obtained in the present study (Table 3) but the plants involved were doubtless not subjected to natural environmental extremes. It should be noted that even in cultivation the cuticle of *O. imbricata* was thinner than that of *O. leptocaulis*, which agrees with the findings of the present study.

The thickness and composition of the cuticle is dependent on a number of internal and external factors. Skoss (1955) showed that cuticular thickness increases with age until the "morphological maturity" of the organ is reached. Sunlight has been repeatedly shown to enhance the amount of cuticle deposition (Hanson, 1917; Brown, 1920; Bright, 1928; Cormack & Gorham, 1953) and the degree of waxiness of the cuticle (Skoss, 1955). There are some indications that ultraviolet radiation may increase cuticle deposition (Martin & Juniper, 1970). Similarly, water stress and high temperature have been reported to cause an increase in the amount of waxiness of plant cuticles (Lee & Priestly, 1924; Skoss, 1955). On the other hand, Kurtz (1958) reported that the cuticles of many desert plants, including a species of *Opuntia*, have a rather low wax content which is

contrary to what would be expected in an environment noted for high insolation, temperature, and water stress.

Some of the possible functions of the cuticle are described by Martin & Juniper (1970). The cuticle may play a part in the support of the plant. It may protect the plant from mechanical damage due to wind borne particles. A thick cuticle may result in increased reflectivity to radiation. Cameron (1970), however, states that reflectivity is due to wax which is deposited on the surface of the cuticle (epicuticular wax) and not to the thickness of the cuticle or the wax impregnating the cuticle.

The major function of the cuticle is generally presumed to be the prevention of water loss. Moreshet (1970) has shown that cuticular resistance to water loss is inversely correlated with the relative humidity of the air and suggests that the changes in cuticular resistance might be reversible. He states that "such an adaptation to changing water stress in the atmosphere would have important implications for plants exposed to conditions of extreme water stress." Such plants would have a high cuticular resistance during dry conditions but might be able to absorb water through the cuticle during moist conditions.

The value of the cuticle as a transpirational barrier is exceedingly variable from species to species. Kamp (1930) found that cuticular transpiration comprised from one-half to less than one-fortieth of the total transpiration of seven species of woody plants. Pisek & Berger (1938), working with a wider variety of plants, measured rates of absolute cuticular transpiration ranging from twice that of Kamp's highest value to one-tenth that of Kamp's lowest value.

It is plain that cuticular transpiration is variable among species, but the cause of this variability is uncertain. Kamp stated that, in general, the chemistry and structure of the cuticle was more important in the determination of the cuticular resistance than the thickness alone. He also showed, however, that among closely related species, cuticular resistance to water loss is correlated positively with cuticular thickness.

It might be presumed, therefore, that those *Opuntia* species in the present study with thicker cuticles also have greater cuticular resistances. This would be advantageous to a plant subjected to periods of prolonged drought. Those *Opuntia* species with the thicker cuticles also have greater levels of ploidy (Table 3). Polyploidy then, with the resulting increased deposition of cuticle, may make some of the opuntiads less likely to desiccate.

Stomatal length.—Anthony (1949, 1956) reported the following average stomatal lengths for *Opuntia* species: *O. imbricata* (20.6 μ), *O. imbricata* var. *argentea* (36.9 μ), *O. kleiniae* (23.3 μ), *O. leptocaulis* (23.6 μ), *O. phaeacantha* (29.5 μ), and *O. lindheimeri* (29.3 μ). With the exception of *O. imbricata* var. *argentea*, these stomatal sizes average about 60% of the stomatal sizes of the same species in the present study. Anthony's results agree with those of the present study in that the chollas often have smaller stomates than do the prickly pears. The discrepancy between the stomatal sizes reported by Anthony and those reported in the present study may be due to her use of leaf peels while stem peels were used here. Schleiden (1845) noted that leaves of *Opuntia* are covered

with stunted or deformed stomates and only rarely showed regularly formed stomates. It may be that there is selection against regular stomatal development on these ephemeral leaves. If this is so, it apparently is not a universal phenomenon in *Opuntia*, since Freeman (1970) stated that stomates on the leaves of *O. basilaris* appeared normal and fully functional. He did not, however, compare stomatal size between leaves and stem.

It is also possible that the apparent discrepancy in the size of leaf and stem stomates has a non-selective basis. Penfound (1931) and Gindel (1969) stated that stomates formed under stress conditions such as high light and/or low soil moisture tend to be smaller than those formed under less stressful conditions. Similarly, Meidner & Mansfield (1968) stated that stomatal size tends to be smaller towards the top of the plant. On the other hand, Bright (1928) and Sharma & Dunn (1968) found stomatal length to be environmentally stable.

In the present study, stomatal length is more stable than any other character measured as indicated by the low average coefficient of variation (9%). This lack of variation is due to genetic control as shown by several facts. First, at all seven of the sites in the within-site comparisons, the chollas have smaller stomates than the prickly pears, thus agreeing with the overall species comparisons. Second, stomatal length was markedly different between the two members of three of the four paired collections, indicating genetic rather than environmental control over stomatal length. Third, at only one of the within-site comparisons (site 3) do the values for all collections fall above or below the average values for their species. This indicates a rather small environmental influence on the expression of stem stomatal length. Thus, while stomatal length may be modified to some extent by environmental conditions, it is for the most part genetically determined and quite stable.

It is in part this stability that has allowed the use of stomatal length or area as an indicator of polyploidy in closely related species. The correlation of ploidy and stomatal size has been established in a variety of plants. Wagner (1954) found such a correlation for diploids, triploids, and tetraploids in the fern genus *Asplenium*; Stone (1961) has shown a correlation between stomatal area and level of ploidy in *Carya*; and Sax & Sax (1937) showed that a correlation exists for diploids and tetraploids of *Tradescantia*.

Such a correlation between ploidy and stomatal size holds only to a limited extent in the species of *Opuntia* examined here. The two prickly pears, which are both hexaploids, do have the largest stomates (ca. 51 μ), but the three cholla species all have small stomates (ca. 35 μ), even though *O. imbricata* is a diploid and *O. leptocaulis* and *O. kleiniae* are tetraploids. The occurrence of smaller stomates than would be expected on the basis of ploidy in *O. leptocaulis* and *O. kleiniae* implies that there has been selection against large stomates in those species. Bearing in mind that these two species are the least massive of those under consideration, and thus have the least water storage capacity, it is easy to imagine strong selective pressures resulting in a reduction in pore size, and thus an increased stomatal resistance and decreased potential water loss. Such a relation-

ship between pore size and diffusion resistance has been demonstrated by Bange (1953).

Although the results of the present study indicate that members of the subgenus *Opuntia* have larger stomates than members of the subgenus *Cylindropuntia*, this is not always the case as shown by Anthony's (1949) study. In addition, Hanks & Fairbrothers (1969) obtained an average stomatal length of about 23 μ for diploid populations of *Opuntia compressa*, subgenus *Opuntia*, in New Jersey. When this is compared with the average stomatal length of about 51 μ for the hexaploid prickly pears of the present study, it is apparent that stomatal size is not strictly related to subgeneric categories but is related in part to the level of ploidy and in part to other factors.

Stomatal density.—Brown (1920) reported a stomatal density of 32 to 36 stomates per mm^2 of surface for *Opuntia blakeana* (= *O. phaeacantha*), which is in perfect agreement with the species average of 35.5 stomates per mm^2 found in the present study. Dittmer (1959), however, reported a density of 11 stomates per mm^2 for *O. imbricata*, which is only about one-sixth of the species mean of 62 stomates per mm^2 found for *O. imbricata* in the present study. Stomatal density is reported to be readily modified by environmental conditions. In most cases, stress conditions such as high light intensity or low water availability tend to increase stomatal density, probably due to a general reduction in the amount of cell expansion during growth of the plant (Brown, 1920; Salisbury, 1928; Penfound, 1931; Gindel, 1969; Sharma, 1972). Bright (1928) found fewer stomates for the most part on more exposed plants than on protected plants. Soule & Lowe (1970) found fewer stomates on the south (more exposed) sides of *Cereus giganteus* plants than were found on the north sides. Arzee & Glinka (1959) found that the water regime of the plant had no effect on the stomatal frequency of corn or cotton leaves.

Stomatal density was found to be very variable in *Opuntia*, coefficients of variation (Table 3) averaging nearly 35%. This variability, however, was not readily attributable to environmental effects. In fact, only at site 14, (Table 9) were the values for all collections below the average value for their respective species. If environmental conditions were the major cause of the high degree of variability seen in stomatal density, one would expect the species at more than one site to show consistent deviations from the overall species norms. On the other hand, stomatal density was markedly different between the two members of only one of the four paired collections, which would tend to indicate environmentally induced similarity between members of the other three paired collections. The relative importance of environmental and genetic effects on stomatal density are, therefore, obscure.

Stomatal density does appear to be inversely correlated with the level of ploidy in groups of related plants. Sax & Sax (1937) stated that tetraploids had a lower stomatal frequency than diploids for a number of species. In the present study, the diploid *Opuntia imbricata* does have the highest stomatal density (62/mm^2) and the hexaploid *O. lindheimeri* and *O. phaeacantha* have the lowest stomatal

densities (35/mm²). The tetraploid *O. leptocaulis*, however, has nearly the same stomatal density (36/mm²) as the hexaploids.

Bange (1953) has shown that stomatal resistance to transpiration decreases with increasing pore size and with increasing stomatal density. Meidner & Mansfield (1968) pointed out that "there is a tendency for stomata to be smaller where they are more numerous." In other words, there appears to be a slight negative correlation between stomatal size and stomatal density. This relationship is seen in some opuntiads. *Opuntia compressa*, for example, has a high density (49/mm²) of small (23 μ long) stomates (Hanks & Fairbrothers, 1969). In the present study, the species with the lowest stomatal densities, *Opuntia lindheimeri* (35.3/mm²) and *O. phaeacantha* (35.5/mm²) have the largest stomates (51 μ and 52 μ), and the species with the highest stomatal density, *O. imbricata* (62.1/mm²) has small stomates (34 μ). *Opuntia leptocaulis*, however, which has equally small stomata (34 μ), has nearly the same low stomatal density (36.5/mm²) as *O. lindheimeri* and *O. phaeacantha*. It may be that there has been selection against high stomatal density in *O. leptocaulis* due to its small mass, as discussed under stomatal length.

It appears that there is strong selection resulting in reduced stomatal transpiration. Killian & Lemée (1956) point out that the succulents in general are noted for a low stomatal density. In the Opuntiae, which do not have exceptionally low stomatal densities, a number of additional resistances are associated with the stomata. The subsidiary cells may extend under the guard cells, narrowing the substomatal passage (Fig. 17), a feature also noted by Bukvic (1912). Freeman (1970) reported subsidiary cells that arched over the stomata in *Opuntia basilaris*, a feature which the present author has seen in two other *Opuntia* species (*e.g. O. streptacantha* and *O. microdasys*). The enlarged crystal-bearing hypodermal cells frequently narrow the substomatal chamber (Fig. 18) in *Opuntia* (Bukvic, 1912; Wolf, 1912) and in the more primitive leaf-bearing cacti *Pereskiopsis* and *Quiabentia* (Bailey, 1964*b*). Finally there is the long, tube-like substomatal chamber itself (Fig. 18) which passes through the collenchymatous hypodermis. All of these must contribute to the transpiration resistance.

Stomatal index.—Salisbury (1928) devised the stomatal index to take into account the variations caused in the stomatal frequency by environmental differences. Since these environmental differences caused changes in epidermal cell frequency corresponding to changes in the stomatal frequency, a ratio of stomates to epidermal cells was found to be more stable than either stomatal or epidermal cell frequency alone. Meidner & Mansfield (1968) and Sharma & Dunn (1968) have agreed with Salisbury's statement that the value of the stomatal index is much more constant within a species than stomatal frequency.

This, however, is not the case with the species under study. The average of the coefficients of variation show that the stomatal indices are as variable (32%) within species as the stomatal frequencies (35%). One cause of this variability is the tendency of the epidermal cells to increase in number by anticlinal division (Boosfeld, 1920). Thus the proportion of stomates to epidermal cells which is

established during development is not maintained but is altered by the continual addition of more epidermal cells.

The significance of the stomatal index lies in the fact that it tends to cancel out variations in stomatal density caused by differences in cell size, such as may be caused by polyploidy. In the present study, in fact, the stomatal index does not correlate well with the level of ploidy, the tetraploid *Opuntia leptocaulis* having the lowest stomatal index (0.6) while the hexaploid *O. phaeacantha* has the highest (1.5) with the diploid *O. imbricata* falling in between (1.0). The results also indicate that the stomatal indices for these species are not free from environmental influences. Stomatal index was not markedly different between the two members of any of the four paired collections. This indicates either a remarkable lack of variability, which the coefficients of variation indicate is not the case, or the influence of the environment. At only two of the seven sites, however, were the values for all collections above (Table 6) or below (Table 4) the average values for their respective species, which is not an indication of strong environmental influences.

Stomatal index, does, however, discriminate between the species to a slightly better extent than does stomatal density. This, plus the relative independence of this character from the level of ploidy, suggest that it may be a characteristic worth measuring for more cacti.

Hypodermis.—The crystal-bearing layer seems to be a universal feature in *Opuntia* and has been noted by a great many authors (Ganong, 1895; Preston, 1901; Bédélian, 1911; Coutant, 1918; Bailey, 1968; Hamilton, 1970*b*). Many of these authors indicate differences in crystal abundance within this layer but whether this is a specific difference or is due primarily to environmental difference is not known. Drastic modifications, such as the complete absence of a crystal layer in etiolated shoots of *Opuntia blakeana* (= *O. phaeacantha*), have been reported (Brown, 1920).

Many functions have been proposed for these hypodermal calcium oxalate crystals. Ganong (1895) felt that they were in part a metabolic by-product which could not be disposed of due to the "lack of falling parts, leaves and bark." He also felt that in certain cases they served as protection against damage from small animals such as snails. Bédélian (1911) felt that the crystals helped reduce evaporation. There is indirect evidence that they are not just a metabolic by-product. Price (1970) has found that the quality and quantity of organelles in druse idioblasts of *Cercidium* (paloverde) "suggest that there is a high degree of activity in the mature idioblasts." It is also notable that the hypodermal druse crystals have a distinct rounded morphology that is quite different than the more typical angular druses which are abundant in the pith and cortex of the Opuntiae (Fig. 19).

The collenchymatous hypodermis is as ever-present in *Opuntia* as is the crystal layer. It develops rather early in the life of the plant (Hamilton, 1970*a*) but has been noted to be absent from etiolated shoots of *O. blakeana* (= *O. phaeacantha*) by Brown (1920). The thickness of this tissue has in the past most commonly been reported in cell layers rather than in micra, which makes

comparisons with the present data rather difficult. Preston (1901) stated that the hypodermis of *O. phaeacantha* was composed of six to eight layers while that of *O. leptocaulis* was four to five layers thick. Bédélian (1911) reported a six-layered hypodermis for both *O. frutescens* (= *O. leptocaulis*) and *O. kleiniae* but a five-layered hypodermis for *O. rosea* (= *O. imbricata*). Coutant (1918) reported *O. discata* (= *O. phaeacantha*) with a hypodermis of five to seven layers thick. Brown (1920) reported a six-layered hypodermis in normal stems of *O. blakeana* (= *O. phaeacantha*). The information from these authors indicates that *O. phaeacantha* has the hypodermis with the most layers but the information is not sufficient to separate the three chollas. In the present study, *O. leptocaulis* and *O. kleiniae* are essentially identical with respect to hypodermal thickness (126 μ), and *O. phaeacantha* has the thickest hypodermis (195 μ).

Boosfeld (1920) indicated that the hypodermis, while variable between species, was not very variable within species. The results of the present study are in agreement with this. Each of the three growth forms, pencil cholla, tree cholla, and prickly pear, are significantly different from one another at the 5% level. The average coefficient of variation (16%) is only half that of the stomatal density or stomatal index. The rather low variability is reflected in the fact that the species at five of the seven sites fall in the same relative positions according to hypodermal thickness as they do in the overall comparisons (Table 3), *i.e.*, the pencil chollas have the thinnest hypodermes and the prickly pears have the thickest hypodermes. This lack of variability is likely due to genetic rather than environmental control since the two members of two of the four paired collections (Tables 4, 10) were markedly different with respect to hypodermal thickness. In addition, at only one site (Table 7), were the values for all collections below the average values for their respective species. These data indicate that the hypodermal thickness is not greatly modified by ordinary environmental differences.

This relative stability is reasonable in view of the statement by Bédélian (1911) that the hypodermal collenchyma serves a support function. Wainwright (1970) has shown in *Ambrosia* that most probably the peripheral collenchyma is one of the major support tissues. This would be doubly true in a succulent plant with relatively high mass and retarded development of the vascular tissue. That the peripheral collenchyma in *Opuntia* is indeed under tension, as would be expected according to Wainwright, was shown by Coutant (1918). The more massive prickly pears also have a thicker layer of collenchyma than the much smaller pencil chollas, which is additional evidence for a supportive function.

The collenchymatous hypodermis may also have a function with regard to water movement. Ganong (1895) felt that it might serve a "water holding" capacity. Bailey (1968) stated "there are no intercellular spaces in the apparently impervious collenchymatous layers, the only means of gaseous communication between stomata and intercellular spaces in the chlorenchyma being through special channels in the collenchyma which are jacketed by thick unpitted walls and which tend to have a tenuous inner lining of cutin." While this limits gaseous exchange, the layers of collenchyma should not prove to be a barrier to water movement since, as noted by Bédélian (1911) and others, the common walls of the

collenchyma cells are conspicuously pitted and water transport could readily occur from cell to cell as well as within the walls themselves. Such water transport is necessary for the maintenance of the crystal layer and the epidermis.

Barrel tracheids.—These cells, apparently of common occurrence in cacti more advanced than the leafy *Pereskia*, are of uncertain origin and function. Bailey (1960) states that those in the leaves of *Pereskiopsis* and *Quiabentia* "may have evolved by modification of ordinary tracheary cells with helical or annular thickenings." Boke (1944) working with stems of *Opuntia cylindrica* states that they "are formed directly from ground parenchyma cells." From their distribution in the stems of the *Opuntia* species of the present study the barrel tracheids do not appear to be of vascular origin.

The barrel tracheids are commonly considered to be water reservoirs (Boke, 1944). Ganong (1895) was not convinced of this role and wondered why the barrel tracheids might be better water storers than "the ordinary pith or cortex cells." Bailey (1966) suggested that the cells might play a part in "strengthening excessively succulent tissues." If this is their function or one of their functions, one would expect to see a correlation between the development of this tissue and the degree of succulence. Such a study has not been made in detail.

Vessel member length.—It has been rather firmly established that the general evolutionary trend in vessel element size has been toward shorter, broader cells (Bailey, 1957). According to these and other criteria, such as pitting patterns and end wall angle, the vessel elements of the primitive leafy cacti are quite advanced, ranging from 150 to 400 μ in length (Bailey & Srivastava, 1962). On the basis of length alone, the vessel elements of *Opuntia* would be considered more advanced than those of the leafy cacti since the average lengths for the five species are all less than 200 μ. The shorter, theoretically more advanced elements, however, occur in the chollas, which are generally presumed to be less advanced than the prickly pears. This apparent discrepancy may only be due to differences in the level of ploidy, with which vessel element length correlates quite well, the diploid *O. imbricata* with the shortest vessels (148 μ) and the hexaploid *O. lindheimeri* with the longest vessels (187 μ).

Vessel element length is relatively constant within species, coefficients of variation averaging about 12% for the five species. However, at only two of the seven sites do the species fall in the same relative positions as they do in the overall comparisons, which would indicate a fairly high degree of variability within the species. This apparent contradiction is probably due to the relatively small magnitude of the differences between the species.

Vessel member width.—The general evolutionary trend in vessel width has been toward broader cells (Bailey, 1957). On the basis of width alone, the vessel elements of these *Opuntia* species could be considered less advanced than those of the leafy cacti, since the range of widths (16 μ–50 μ) is considerably less than the range of 20 to 200 μ reported by Bailey & Srivastava (1962). Bailey and Srivastava imply that the narrowest vessels they found were about the same diameter as the cambial initials and that it was the failure of the cambial derivatives to enlarge

during development that resulted in these narrow vessels. Bailey (1957) stated that the dwarfing of vessel size is due to retarded growth in unfavorable habitats.

Carlquist (1961), on the other hand, stated that extremely narrow vessels are probably specialized. If one accepts this view, then the narrow (20–25 μ) vessels of the chollas are more specialized than those of the prickly pears (35–38 μ). In this case, the narrower vessels may increase the tension with which water is held within the plant and thus serve to retard the movement of water (Wind, 1955).

The correlation of stomatal size with vessel width supports the idea that narrow vessels in the chollas are a specialized feature. It might be supposed that vessel member width, like guard cell length, should correlate positively with the level of ploidy. In both cases in the present study, vessel member width and guard cell length, the values for the tetraploid pencil chollas *O. leptocaulis* and *O. kleiniae* were less than would be expected on the basis of ploidy. In both cases, vessel member width and guard cell length, selection pressures may have restricted the size of these cells in these species that have relatively little water storage capacity.

The relative roles that genetic and environmental limitations play in the production of the narrow vessels observed in the opuntiads is not known. Vessel member width is no more variable within species than is vessel member length, coefficients of variation averaging 14% for the five species. At six of the seven sites in the within-site comparisons, the species fall in the same relative positions according to vessel member width as they do in the overall comparisons (Table 3) indicating this lack of variability. At one site, the values for all collections were above the average values for their species, while at three sites, the values for all collections were below the average values for their species. This indicates an environmental control rather than a genetic control. Comparisons of vessel member dimensions with the dimensions of cambial initials in these species are needed to compare with the similar studies in the leaf-bearing cacti by Bailey & Srivastava (1962).

Vessel element length/width (l/w) ratio.—The l/w ratio of an 'advanced' type of vessel element is low since the element would be short and broad. A less 'advanced' type of vessel element would be long and narrow, and thus have a high l/w ratio. With regard to this characteristic the five species fall into the expected phylogenetic positions, the two pencil chollas with the highest ratios (8.5 in *O. leptocaulis* and 7.1 in *O. kleiniae*) and the two prickly pears with the lowest ratios (5.2 in *O. phaeacantha* and 5.0 in *O. lindheimeri*).

Although the l/w ratio is more variable within species than vessel element length or width, coefficients of variation averaging nearly 21%, the species at six of the seven sites still fall in the same relative positions according to l/w ratio as they do in the overall comparisons. The relative positions of the five species with regard to l/w ratio are the same as the relative positions with regard to width alone but not the same as the relative positions with regard to vessel element length. The biological significance of the l/w ratio, if any, is unknown.

Circumference/area (c/a) ratio.—Circumference/area ratios are rather variable within a species, coefficients of variation averaging about 22% for the five species. Nevertheless, the species at four of the seven sites fall in the same relative positions

according to c/a ratio as they do in the overall comparisons. The c/a values were markedly different between the two members of two of the four paired collections, indicating genetic control of c/a ratio. This supports the idea that the c/a ratio is of biological significance, especially when dealing with a group of closely related plants. A plant with a low c/a ratio has an immediate advantage over a plant with a higher c/a ratio with regard to water loss problems. The plant with a low c/a ratio has a smaller proportion of surface area per unit volume and thus a smaller potential water loss per unit volume. Characteristics which correlate with the c/a ratio thus might be assumed to relate directly or indirectly to water loss phenomena.

The c/a ratio is not related to chromosome number since the diploid and hexaploid species have low ratios but the tetraploid species have high ratios. The c/a ratio is not correlated with cuticular thickness (Table 11). This might indicate that those species with a very thick cuticle do not have an appreciably smaller cuticular transpiration rate than those species with the thinner cuticles or that cuticular transpiration rates are insignificant even in those species with thinner cuticles. It also supports the idea that cuticular thickness in these cacti is influenced primarily by the level of ploidy. It would also indicate that the cuticle probably does not play a major role in mechanical support since the more massive species with low c/a ratios do not always have the thickest cuticles.

There is a negative correlation between stomatal length and the c/a ratio (Table 11). Thus the more succulent plants with a lower c/a ratio tend to have the larger stomates. This might indicate, as discussed previously, that a selection against large stomates is operating on the less succulent pencil chollas. This selection has kept the stomatal size of the tetraploid pencil chollas equal to that seen in the diploid *O. imbricata*. It is worth noting that *O. kleiniae*, which is more succulent than *O. leptocaulis*, does have slightly larger stomates. This difference, while not significant at the 5% level, is a point in favor of this hypothesis.

There is no significant correlation between c/a value and stomatal density (Table 11). This is probably due to the fact that four of the five species are not significantly different from one another at the 5% level with regard to stomatal density.

A negative correlation exists between stomatal index and c/a ratio. The more succulent species, which have lower c/a values, have a greater proportion of stomates to epidermal cells than do those species which are less succulent. This may indicate a tendency for the repression of stomates in the less succulent species.

There is a negative correlation between hypodermal thickness and c/a value. The more succulent and more massive species have lower c/a ratios but thicker hypodermal layers. This is in accord with the hypothesis that the collenchymatous hypodermis serves primarily as a supportive tissue.

There is no correlation between vessel member length and c/a ratio. This may be due to the relatively small differences in vessel member length between the species with the shortest vessel members and the species with the longest vessel members. It may, however, indicate that the vessel member length in these species

is not important with regard to the survival of the plant. Differences in vessel element length in these species may be due primarily to the level of ploidy.

There is, however, a negative correlation between vessel width and c/a ratio (Table 11). This is a further indication that it is advantageous for the least succulent species to have the narrowest vessels. Here, as was the case with stomatal length, it appears that the tendency of polyploidy to cause increased cell size has been overridden by selection pressures.

Anthony (1954, 1956) stated that the chollas of the Big Bend region of Texas were less variable than the prickly pears with regard to such morphological characteristics as habit of growth, size of stem joints, and spine color, size, form, and number per areole. This is not true of the anatomical features examined in this study. If the coefficients of variation for each character in Table 3 are averaged for each species, virtually no difference is found between the two subgenera, *Cylindropuntia* averaging 22.9 and *Opuntia* averaging 22.8. There are slight differences between species but the most variable (*O. lindheimeri*, 26.1) and least variable (*O. phaeacantha*, 19.4) species are both prickly pears. With respect to the totality of anatomical characteristics considered here, it is probably correct to say that of these five species, no one species, growth form, or subgenus is more variable than any other.

This lack of any real difference in the degree of anatomical variability between the subgenera is hard to reconcile with Anthony's 1954 paper in which she stated that "Populations which seem to have little genetic variability, *i.e.*, most of the Cylindropuntiae group in this region, usually have greater habitat restriction because they lack variants adapted to diverse environmental conditions." Yet *O. kleiniae* and *O. lindheimeri*, which she stated show a "high degree of ecological restriction" are neither more nor less anatomically variable than *O. phaeacantha*, *O. imbricata*, or *O. leptocaulis*, which she implies have more flexible ecological requirements. It is, of course, possible that the morphological variability with which Anthony was concerned is more important to the survival of these plants than anatomical variability. Still, one would expect such significant morphological variability to be mirrored by the anatomical variability of the characters considered here.

Many of these anatomical characters show continuations of trends of specialization begun in the leaf-bearing Cactaceae. The crystalline hypodermis and the collenchymatous layers are absent in many species of *Pereskia* but are seen in more or less rudimentary form in other species (Bailey, 1961). *Pereskiopsis* and *Quiabentia*, presumably primitive members of the sub-family Opuntioideae, are "characterized by having collenchymatous layers and a well developed crystalliferous hypodermis subtending the epidermis" of the stems (Bailey, 1964*b*). These changes, according to Bailey (1964*a*), are correlated with increasing succulence and "changes in the stature and habits of growth." This is in complete agreement with the trend in hypodermal thickness seen in the present study. Similarly, barrel tracheids are absent from the leaves of *Pereskia* but present in *Pereskiopsis* and *Quiabentia* (Bailey, 1960) and *Opuntia*.

There is also a general trend from the pereskiads through the tribes Opuntiae

and Cereae "toward increasing the circumference of the eustele with concomitant expansion of the pith during later ontogenetic stages of the development of the primary body" (Bailey, 1964*a*). This supports the idea that the pencil chollas with their small piths, as typified by *O. leptocaulis*, are the most primitive members of the genus *Opuntia* (Preston, 1901).

These trends in the development of the hypodermis and increase in pith size are not continued throughout the Cactaceae however. Darbishire (1904) reported no collenchymatous hypodermis in *Mammillaria elongata*, and Bailey (1968) stated that a structurally homologous form of crystalline hypodermis does not occur in the subfamily Cereoideae. In many of the more advanced members of the family, such as *Mammillaria* and *Echinocereus*, the pith occupies a rather small proportion of the cross section of the stem, in many cases a smaller proportion than is the case in some of the *Opuntia* species.

The trends in hypodermal development and change in size of the eustele provide opportunities for further study in the opuntiads as well as in other cacti. In 1901, Preston (1901) stated: "Schumann has hinted rather strongly at the connecting links between *Opuntia* and *Cereus*; anatomical studies may give more definite information upon this point." In 1944, Boke (1944) expressed the same feelings about the Cactaceae: "a greater knowledge of anatomy and development may do much to clarify systematic relationships." The statement still holds true today.

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ADDITIONAL PANAMANIAN MYRISTICACEAE

Alwyn H. Gentry[1]

Abstract

Recent collections from wet forest areas of Panama include several species of Myristicaceae new to science or to the North American continent. The two new species described below are of special interest as having the largest fruits in their respective genera.

Virola

1. **Virola megacarpa** A. Gentry, sp. nov.—Fig. 1.

Arbor dioecius, foliorum trichomatibus stellatis, nervis secondariis numerosis confertis *V. multinerviae* affinis, a quo fructibus multo majoribus differt; fructibus majoribus a congeneribus diversus.

Medium-sized to large dioecious tree; branchlets densely stellate-pubescent, glabrescent with age. Leaves subcoriaceous; upper surface essentially glabrous except for the stellate-puberulous midvein, sometimes with a few widely scattered stellate trichomes, lower surface strongly and persistently stellate pubescent with stalked trichomes; oblong, (11–)29–37 cm long, (4.5–)7–13.5 cm wide, rounded to subcordate at base, cuspidate-acuminate at apex, the acumen usually 1–2 mm long; the costa plane above, very prominent below, secondary nerves slightly impressed above, prominent below, 36–43 per side (average 38.9, mode 40), close together, 11–20 per 10 cm (average 14 per 10 cm); petiole 0.8–1.3 cm long. Male inflorescence not seen. Female inflorescence (in fruit) stellate-pubescent, to 8 cm long, once forked or with a single pair of lateral branches near the middle, each of the two or three main branches bearing a single fruit. Fruit pedicellate, pedicels stout, 7–12 mm long; ovoid-ellipsoid, 4.5–6 cm long, 2.7–3 cm wide, base obtuse, apex bluntly pointed, densely and persistently rufous-pubescent with trichomes to ca. 0.8 mm long, the trichomes variously stellate or dendroid, usually with short lateral branches; the pericarp 5–8 mm thick; the aril laciniate to base (very immature fruits of *Nee 7920* 30–35 mm long).

Type: Panama. colón: Santa Rita Ridge; tree 15 m, fruits brown, pubescent, 23 March 1972, *Gentry & Dwyer 4804* (MO, holotype; isotypes to be distributed).

Additional collections examined: Panama. colón: East Ridge (= Santa Rita Ridge), large tree, the latex ultimately oxidizing reddish-brown; would key to *Virola* in Fl. of Panama, but obviously fits none of these, fruits 1–2, rufous-tomentose, to 6 cm, 23 Feb 1968, *Duke 15261* (MO, to be distributed). panamá: Premontane wet forest area, El Llano-Carti Road, 5 km N of Pan-Am Hwy. at El Llano, ca. 300 m, tree 12 m, wood soft, carpels fuzzy brown, one-seeded, 10 Nov 1973, *Nee 7920* (MO, WIS, to be distributed).

This species belongs in A. C. Smith's (1937) group Rugulosae because of the stalked and persistent trichomes of the lower leaf surface and the thick fruit pericarp. Vegetatively it could be allied with *V. multinervia* Ducke, *V. koschnyi* Warb., *V. albidiflora* Ducke, or *V. duckei* A. C. Smith. However, the remarkable

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fruit of *V. megacarpa* distinguishes it at once from all other species of group Rugulosae. Its fruit is nearly twice as long as that of most related species. The largest fruit described by Smith for a species of this alliance, that of *V. albidiflora*, is 30–38 mm long and has a 4–6 mm thick pericarp but is glabrous. The fruits of other related species described by Smith reach only 25–30 mm in length. *Virola decorticans* Ducke of Amazonian Peru and adjacent Brazil is most similar to *V. megacarpa* on the basis of its ovoid-ellipsoid, persistently tomentose, 24–35 mm long fruits but has upper leaf surfaces pilose with simple or forked trichomes.

Nine additional species of *Virola* have been described since Smith's monograph. Two of these later proved referable to other genera but most of the rest were ascribed to the Rugulosae group. Two of these more recently described species have relatively large fruits. *Virola dixonii* Little of Ecuador has thick-valved fruits to 4 cm long but has smaller leaves (13–25 cm by 3.5–6 cm) with acute bases. *Virola kukachkana* L. Wms. of Amazonian Peru has glabrous fruit 3–3.5 cm long and also has much smaller leaves. No other species approaches *V. megacarpa*.

Among Panamanian species, *V. megacarpa* would key out with *V. koschnyi* from which it differs chiefly in its much larger, more persistently pubescent fruit with a thicker pericarp. Vegetatively it differs from *V. koschnyi* in its more closely spaced and more numerous secondary nerves (18–35 per side in *V. koschnyi*).

2. **Virola surinamensis** (Rol.) Warb., Nova Acta Acad. Caes. Leop.-Carol. German Nat. Cur. 68: 208. 1897.

Virola surinamensis, previously known as a common species of the Guiana region has already been reported from Panama on the basis of a single sterile collection (Dwyer, 1972). During routine curation I re-determined the specimen cited by Dwyer as *V. nobilis* A. C. Smith, the Panamanian species related to *V. surinamensis*. However, a re-examination of the status of *V. nobilis* indicates that it should be regarded as synonymous with *V. surinamensis*.

Smith (1937) noted that *V. nobilis*, then known only from the Panama Canal Zone, was closely related to *V. surinamensis* from which it was distinguished primarily by a larger fruit distinctly stipitate at the base. He also commented on the distinct ranges of the two species, *V. surinamensis* being known from the Guiana region, Lesser Antilles and coastal Brazil. In addition some vegetative secondary characters were used to separate these two species in his key: secondary nerves 17–23 per 10 cm, leaf surfaces dull in *V. nobilis*; secondary nerves 12–18 per 10 cm, upper leaf surfaces often shining in *V. surinamensis*. Much more complete material of *V. nobilis* is now at hand than was available to Smith and most of the characters thought to characterize *V. nobilis* do not hold. The secondary nerves of the Panamanian specimens I have examined vary from 9–19 per 10 cm and average 14 per 10 cm, just as in *V. surinamensis*. Fruits of some Panamanian collections are indistinctly stipitate (*e.g.*, *Tyson et al.* 3753 and *Croat 8090* (both MO)) while those of one collection (*Croat 11462*) are completely estipitate. Upper leaf surfaces of *V. nobilis* appear to be uniformly dull but those of the majority of specimens of *V. surinamensis* at MO are similarly dull. *Virola*

nobilis also proves to be more common on Cerro Jefe, east of the Canal Zone, than in the Canal Zone itself and may be regarded as part of the distinctive Cerro Jefe vegetation which is known to include a number of disjunct Guianan elements, some specifically distinct (*e.g.*, *Roupala percoriacea* A. Gentry, *Brysonima dressleri* W. Lewis) and some not (*e.g.*, *Aspidosperma markgravianum* Woods.). This established pattern of disjunction lessens the taxonomic importance of the range separation of *V. nobilis* and *V. surinamensis*. Only fruit size remains a potential character to distinguish *V. nobilis* from *V. surinamensis* and even here the two species overlap (19–32 mm by 14–22 mm in *V. nobilis*; 13-21 mm by 11–18 mm in *V. surinamensis*). *Virola nobilis* is best treated as a synonym of *V. surinamensis*.

IRYANTHERA

Although the genus is unreported for North America, three species occur in the Colombian Choco and might also be expected in Panama (Smith, 1950). Two of these have now been collected in Panama along with a distinctive new species of this genus.

3. **Iryanthera juruensis** Warb., Verh. Bot. Vereins Prov. Brandenburg 47: 137. 1905.

A single fruiting collection from Panama appears to be referable to this species. This is *Holdridge 6267* (MO) collected at Camp Betija, Donoso District, Colón Province, 60–150 m elevation. It is described as a tree 20 m tall, 30 cm dbh., fruits wider than long, borne on the heavier leafless branches. It was determined as *I.* aff. *juruensis* by John Dwyer and is a good match for South American material of that species at MO annotated by A. C. Smith. There seems to be no doubt as to its identity. *Iryanthera juruensis* differs from *I. ulei* and from the new species described below in the inconspicuous intramarginal anastomoses of its leaves. It has rounded fruit extremities in contrast to the pointed extremities of *I. ulei* and a much smaller fruit than *I. megistocarpa*.

4. **Iryanthera ulei** Warb., Verh. Bot. Vereins Prov. Brandenburg 47: 137. 1905.

A single collection from Darién Province keys to *I. ulei* and agrees with specimens of that species at MO. The Panamanian collection is *Duke 8764* (MO) from Río Balsa between Ríos Areti and Manene. It is described as a shrub with cream flowers. The leaves are narrowly oblong-elliptic or obovate-elliptic, glabrous, secondary nerves impressed above and raised beneath, 14–20 per side, spreading and clearly anastomosing near margin. The male inflorescence is an axillary raceme, 4–9 cm long, several from each node, the flowers in subsessile clusters of 2 or 3, the pedicels ca. 3 mm long, rachis and pedicels strigose with malpighiaceous trichomes and the bracteole one-sided, ca. 0.5 mm long. The androecium is ca. 0.8 mm long, the filament column columnar, not swollen at base, anthers ca. 0.2 mm long, filament column 0.5–0.6 mm long, 0.2 mm diameter, glandular and slightly contracted at base.

FIGURES 1–2. New species of Myristicaceae.—1. *Virola megacarpa* A. Gentry. Photo of type collection (*Gentry & Dwyer 4804*).—2. *Iryanthera megistocarpa* A. Gentry. Photo of type collection (*Gentry, Mori & Kallunki 14200*).

5. **Iryanthera megistocarpa** A. Gentry, sp. nov.—FIG. 2.

Arbor dioecius, foliorum nervatura *I. ulei* affinis, laminis nigro-punctatis differt; fructibus majoribus a omnibus aliis speciebus differt.

Dioecious tree to at least 15 m tall; branchlets inconspicuously sericeous with malpighiaceous trichomes, glabrate. Leaves chartaceous to subcoriaceous, narrowly elliptic, the base more or less rounded, apex tapering, acute or acuminate, upper surface glabrous, lower surface with a few scattered malpighiaceous trichomes, 11–17 cm long, 4.2–7 cm wide; the midvein raised above, prominent below, secondary nerves impressed above, raised below, 12–16 per side, spreading, clearly anastomosing near the margins, the veinlets immersed, the surface relatively smooth with scattered darker minute glandular areas, these appearing macroscopically punctate; petiole 1–2 cm long, canaliculate. Fruiting inflorescences unbranched, 2–4 cm long, fruits 1 per inflorescence, pedicel ca. 5 mm thick; fruit (only immature seen) ellipsoid to subglobose, 4–5 cm long, 3.5–4 cm wide, slightly to noticeably carinate, lateral extremities not developed, the surface conspicuously wrinkled-rugose, more or less glabrous, the pericarp ca. 6 mm thick.

TYPE: PANAMA. PANAMÁ: El Llano-Carti Road, 18 km from Pan-Am Hwy., tropical wet forest, 330–370 m, tree 20 m, fruits green, immature, to 5 cm diameter, typical myristicaceous branching, 14 Feb 1975, *A. Gentry, S. Mori & J. Kallunki 14200* (MO holotype; isotypes to be distributed).

Additional collections examined: PANAMA. PANAMÁ: 14 km above Pan-Am Hwy. on road from El Llano to Carti-Tupile, 200–500 m, tree over 8 m, fruit green, rugose, soft, inner part soft semi-translucent, whitish, flavor astringent semi-sweet, leaf pale green below with black irregular dots, 20 Feb 1973, *Kennedy 2515* (MO, to be distributed). Primary forest along newly cut road from El Llano to Carti-Tupile, 12 mi above Pan-Am Hwy., 200–500 m, tree 15 m, fruits green, ± globose, ca. 5 cm diam., 13 Mar 1973, *Croat 22895* (MO, to be distributed). Camino de Llano a Carti, approximadamente entre los 14 a 18 kms de la carretera a Chepo, ± 400 m, 20 Feb 1973, *Correa, Dressler, Carrasquilla & Mendieta 1873* (MO, PMA). 16–20 km above Pan-Am Hwy. on road from El Llano to Carti-Tupile, ca. 400 m, tree over 5 m, fallen down, fruit fleshy, rubbery, shiny green, 28 Feb 1973, *Kennedy 2704* (MO).

My first inclination was to identify these fruiting collections with the flowering specimen referred above to *I. ulei*. The leaves are quite similar especially in the conspicuous marginal anastomoses, but those of *I. ulei* lack the characteristic punctate appearance of *I. megistocarpa*. Microscopically the lower leaf surfaces of both *I. ulei* and *I. juruensis* also have a characteristically rough, almost subpapillate, texture which is different from the smoother surfaces of *I. megistocarpa*.

The fruits of this species are longer than any described by Smith (1937). Only juvenile fruits have been observed and it may be supposed that the mature fruits of *I. megistocarpa* may take the transversely ellipsoid shape characteristic of the genus and thus be significantly broader than described here. Only *I. grandis* Ducke of Amazonian Brazil has fruits approaching in size (3.5–4.3 cm by 4.5–5 cm) those of *I. megistocarpa*. That species has much larger leaves and more secondary nerves with inconspicuous marginal anastomoses. Its pericarp is even thicker (7–11 mm) than in *I. megistocarpa*. The only species of the genus described since Smith's monograph (*I. microcarpa* Ducke = *I. tessmannii* Mgf.) is *I. megistophylla* A. C. Smith from the Colombian Choco. This species has

similar fruits 3.5–4 cm long and 5 cm broad but very different, giant leaves 28–40 cm long and 10–14 cm wide.

The three Panamanian species of *Iryanthera* may be distinguished by the following key.

a. Leaves black-punctate beneath, with a few scattered trichomes, secondary veins below distinctly anastomosing near the margins; fruit more than 4 cm long ..... *V. megistocarpa*
aa. Leaves not black-punctate beneath, glabrous, secondary veins below distinctly or indistinctly anastomosing; fruit less than 2 cm long.
  b. Secondary veins distinctly anastomosing near the margins; fruit extremities pointed; filament column not swollen at base ..... *I. ulei*
  bb. Secondary veins not distinctly anastomosing near the margins; fruit extremities rounded; filament column usually swollen at base ..... *I. juruensis*

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STUDIES IN BIGNONIACEAE 17: *KIGELIANTHE*: A SYNONYM OF *FERNANDOA* (BIGNONIACEAE)[1]

ALWYN H. GENTRY[2]

Kigelianthe of Madagascar is not separable from *Fernandoa* of continental Africa. The two genera seem to have been maintained separate as the result of a combination of historical accident and botanical provincialism. In fact the affinity of *Kigelianthe* with *Fernandoa* has never even been mentioned in the literature. A brief history of the situation may help in its clarification.

Fernandoa (sphalm *Ferdinandia*) was described by Seemann in 1865 as a new genus of Tecomeae with the single species *F. superba* based on a collection of Welwitsch from Angola. In 1870 Seemann described a second species from East Africa as *F. magnifica* (sphalm *Ferdinandoa*) and in 1911 Gilg and Mildbraed described a third species from the Belgian Congo (Zaïre) as *Ferdinandia adolfi-friderici*. A fourth species, *Ferdinandia mortehani* De Wild, is probably not distinct from *F. adolfi-friderici*. The plethora of mispellings of *Fernandoa* (*Ferdinandia, Ferdinandoa, Ferdinandia, Ferdinanda, Ferdinandio, Ferdinandi*), including that of the original description, is discussed by Milne-Redhead (1949) who also pointed out that the corrected spelling of the genus means the combination *Fernandoa ferdinandi*, based on Welwitsch's *Bignonia ferdinandi*, is not a tautonym and should be adopted for the type species. Sillans (1951, 1953) later described *Tisserantodendron* as a new genus of Central African Bignoniaceae with two species, one from Gabon and one from Oubangui-Chari (Central African Republic). Heine (1964) discovered that Sillans' genus was synonymous with *Fernandoa* and its two species synonymous with the two Equatorial African *Fernandoa* species.

Meanwhile Baker (1881) had discovered a new species of Bignoniaceae from Madagascar in a collection of plants made by L. Kitching. He described it, in the absence of fruit, in the indehiscent-fruited tribe Crescentieae as *Kigelia madagascariensis*. Baillon (1888) described *Kigelianthe* as a new genus of Tecomeae endemic to Madagascar from material, including fruits, collected by Grevé and Hildebrandt but in fact representing the same species as *Kigelia madagascariensis*. Baillon thought this material to represent two species but Perrier de la Bathie (1938*a*, 1938*b*) considered these to be varieties. Baker (1888) and Scott Elliot (1890) described two more species of this genus from Madagascar under *Colea* (tribe Crescentieae) and these were transferred to *Kigelianthe* by Perrier de la Bathie as *K. macrantha* and *K. coccinea*. Sprague (1904) pointed out that Baker's *Kigelia madagascariensis* rightly belonged in *Kigelianthe*.

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[1] The impetus for this paper came from a visit to Madagascar sponsored by a National Geographic Society grant to Dr. Peter Goldblatt, Missouri Botanical Garden. The resultant opportunity of seeing *Kigelianthe* in flower first called my attention to its similarity with *Fernandoa*.

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Kigelianthe was compared to the very different Asian *Radermachera* by Baillon who apparently had seen no specimens of *Fernandoa* and based his concept entirely on Seemann's plate. That all essential characters of his *Kigelianthe* agreed with those of *Fernandoa* was overlooked by Baillon and all subsequent authors. Both genera have large, irregularly-several-labiate calyces; large, campanulate, red-orange (yellow in one species of *Fernandoa*) corollas; subexserted stamens; linear, subterete, longitudinally-striate capsules dehiscing perpendicularly to a flat septum; imparipinnately compound leaves; large discs; ovules many-seriate in each locule; and thin, usually, bialate seeds. In fact the two genera are so similar that *F. magnifica* probably has more in common with *K. madagascariensis* than with *F. adolfi-friderici*. Both genera have three species and include dry forest shrubs or small trees (*K. madagascariensis*, *K. macrantha*, *F. magnifica*) and taller moist forest trees (*K. coccinea*, *F. adolfi-friderici*, *F. ferdinandi*). The only character, and that an insignificant one, by which the two genera could be morphologically separated appears to be the less broadly campanulate corollas of the Madagascar species.

Why was the close relationship of these striking plants overlooked for so long? Chance played a part: had the species of *Kigelianthe* not all been originally described without fruiting material their relationships might have been sought in the Tecomeae rather than the Crescentieae; had Baillon seen material of *Fernandoa* he might have realized its identity with his proposed new genus. A kind of botanical provincialism seems to have been partially responsible for some of the problems. Species of both genera were first described by English botanists and subsequently redescribed with a new generic name by French botanists. In each case a second French worker corrected the oversight of his predecessor. But no one familiar with the Bignoniaceae of either Madagascar or continental Africa seems to have looked critically at the plants of the other region.

Placing *Kigelianthe* in synonymy under *Fernandoa* brings the number of species in that genus to six making it rather large by Bignoniaceae standards (*cf.* Gentry, 1973). The three new combinations needed in *Fernandoa* are:

1. **Fernandoa coccinea** (Scott Elliot) A. Gentry, comb. nov.

Colea coccinea Scott Elliot, Jour. Linn. Soc. Bot. 29: 36. *t.* 9. 1890.
Kigelianthe coccinea (Scott Elliot). H. Perr., Ann. Mus. Col. Marseille, ser. 5, 6: 19. 1938.

Distribution: Eastern Madagascar north to vicinity of Fenerive.

2. **Fernandoa macrantha** (Baker) A. Gentry, comb. nov.

Colea macrantha Baker, Jour. Linn. Soc. Bot. 25: 337. 1888.
Kigelianthe macrantha (Baker) H. Perr., Ann. Mus. Col. Marseille, ser. 5, 6: 19. 1938.

Distribution: Ambongo-Boina region of western Madagascar (vicinity of Majunga).

3. **Fernandoa madagascariensis** (Baker) A. Gentry, comb. nov.

Kigelia madagascariensis Baker, Jour. Linn. Soc. Bot. 18: 274. 1881.
Kigelianthe grevei Baill. ex K. Schum. in Engl. & Prantl, Natürl. Pflanzenfam. 4(3b): 244. 1894. nom. nud.

Kigelianthe hildebrandtii K. Schum. in Engl. & Prantl, Natürl. Pflanzenfam. 4(3b): 244. 1894. nom. nud.
Kigelianthe madagascariensis (Baker) Sprague ex H. Perr., Ann. Mus. Col. Marseille, ser. 5, 6: 20. 1938.
Kigelianthe grevei Baill. ex H. Perr., Ann. Mus. Col. Marseille, ser. 5, 6: 20. 1938. pro. syn.
Kigelianthe hildebrandtii Baill. ex H. Perr., Ann. Mus. Col. Marseille, ser. 5, 6: 20. 1938. pro. syn.
Kigelianthe madagascariensis var. *hildebrandtii* Baill. ex H. Perr., Ann. Mus. Col. Marseille, ser. 5, 6: 21. 1938.
Kigelianthe madagascariensis var. *grevei* Baill. ex H. Perr., Ann. Mus. Col. Marseille, ser. 5, 6: 21. 1938.

Distribution: Lowland western Madagascar from vicinity of Antsohihy in the north to Cap Sainte-Marie in the south.

The three previously recognized species of *Fernandoa* are:

4. **Fernandoa ferdinandi** (Welw.) Milne-Redhead, Kew Bull. 1948: 170. 1949. (see Heine, 1964, for synonymy).

Distribution: West Equatorial Africa: Gabon, Angola.

5. **Fernandoa adolfi-friderici** (Gilg & Mildbraed) Heine, Adansonia, n.s. 4: 469. 1964. (see Heine, 1964, for synonymy).

Distribution: Equatorial Africa: Zaïre, Oubangui-Chari (Central African Republic), Cameroun.

6. **Fernandoa magnifica** Seem., Jour. Bot. 8: 280. 1870. (see Milne-Redhead, 1948, for synonymy).

Distribution: Lowland East Africa: Kenya, Tanzania, Mozambique, Rhodesia.

Perichlaena, a monotypic genus endemic to northwest Madagascar is also closely related to *Fernandoa*. It is separated by its scandent habit; more strongly bilabiate corolla; ovules 2-seriate in each locule; shorter, flattened, non-striate fruit; and seed wing surrounding the seed body. These characters seem adequate for generic separation.

In flower *Fernandoa* may be distinguished from other African genera of Bignoniaceae by the large, campanulate, red to yellow corolla, similar to that of the African Tulip Tree (*Spathodea*) and by the irregularly-several-labiate (not spathaceous) calyx. In fruit it is unique among African/Madagascar bignons in possessing a slender, subterete capsule dehiscing perpendicularly to a thin flat septum.

The species of *Fernandoa* may be distinguished by the following key[3].

a. Corolla relatively small, 20–25 mm long; flowers yellow ..... *F. adolfi-friderici*
aa. Corolla large, 50 cm or more long; flowers red-orange or orange-red with yellow in throat (a rare yellow-flowered form of one species also known).
  b. Ovary tomentose; leaves densely and finely tomentose below; western Equatorial Africa ..... *F. ferdinandi*
  bb. Ovary glabrous; leaves often glabrous or glabrescent; eastern Africa or Madagascar.

[3] I have seen no specimens of *F. ferdinandi* and *F. macrantha*; the key characters are taken from the literature.

c. Corolla very broadly campanulate; inflorescence a racemose cyme; pedicels more than 4 cm long; East Africa ..... *F. magnifica*

cc. Corolla less broadly campanulate; inflorescence a paniculate cyme; pedicels less than 2 cm long; Madagascar.

d. Corolla with sessile glands at base of stamens; fruit with 16 longitudinal ribs; seed wings reduced, essentially lacking ..... *F. macrantha*

dd. Corolla with stalked glands or long trichomes at base of stamens; fruit finely striate; seed wings well developed.

e. Anther thecae divergent; corolla with short, gland-tipped trichomes at level of stamen insertion ..... *F. coccinea*

ee. Anther thecae parallel; corolla with long trichomes at level of stamen insertion ..... *F. madagascariensis*

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FLACOURTIACEAE NEW TO PANAMA: *CASEARIA* AND *XYLOSMA*

THOMAS B. CROAT[1]

ABSTRACT

Casearia guianensis (Aubl.) Urban var. *rafflesioides* Croat is described as new. It differs from the typical variety in having precocious flowers and in bearing branch-spines. *Casearia stjohnii* Johnston is considered only a variety of *Casearia guianensis*. It differs from both the typical variety and var. *rafflesioides* in having stouter, more densely pubescent pedicels, longer, darker-colored bracts, and by flowering later in the season. *Xylosma sylvicola* Standley and *X. chloranthum* Donn. Sm. are reported new to Panama.

In the course of field work for the new Barro Colorado Island Flora, three interesting flacourtiaceous plants were encountered. After extensive field observations as well as library and herbarium studies, it is concluded that two are species new to Panama and that one is an undescribed taxon.

CASEARIA Jacq.

Casearia guianensis (Aubl.) Urban is a wide-ranging species occurring in seasonally dry areas and known from the West Indies, Costa Rica, Panama and northern South America. In Panama, where I have observed the species in the field, plants usually flower precociously or at least before leaves are fully developed. Sometimes even the fruits are fully mature before the leaves are completely expanded. In addition to var. *guianensis*, two additional varieties are now known from Panama. The following key distinguishes them.

KEY TO VARIETIES OF *Casearia guianensis*

a. Bracts of the inflorescence dark, thick and opaque, usually more than 2 mm long; pedicels thick, more than 0.5 mm in diameter when dry, densely tomentose, usually hidden by the bracts; in Panama flowering June and July with fruits maturing August and September ---------- 3. var. *stjohnii* (Johnston) Croat

aa. Bracts of the inflorescence pale, whitish to translucent, usually less than 2 mm long; pedicels slender, usually less than 0.3 mm in diameter when dry, sparsely pubescent, usually clearly exposed above the bracts; in Panama flowering March to June with fruits maturing April to June.

b. Leaves elliptic (rarely obovate), mature at time of flowering, drying green on flowering collections, blades to 7.5 (9.5) cm long and to 2.5 (4.5) cm wide; stipules deltoid to narrowly triangular, 1.5–2 mm long; branchlets frequently ending in a stout, sharp, branch-spine; pedicels usually articulate at about the middle ---------- 1. var. *rafflesioides* Croat

bb. Leaves obovate, usually very young or even absent at time of flowering, drying blackish on flowering collections, blades of at least the larger leaves more than 9.5 cm long and 4.5 cm wide; stipules narrowly triangular to subulate, 2–5 mm long; branchlets lacking branch-spines; pedicels usually articulate well below the middle ---------- 2. var. *guianensis*

1. **Casearia guianensis** (Aubl.) Urban var. **rafflesioides** Croat, var. nov.—FIGS. 1–3.

Differt a var. *guianensis* et var. *stjohnii* saepe ramis validis acutis spiniformibus (etiam trunco inferiore armato); lamina ovata vel elliptica, raro obovata vel oblanceolata, apice

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acuminato vel acuto vel rotundato, basi obtusa vel attenuata et decurranti, 2.5–11 cm longa, 1–3.4 cm lata; stipula deltoidea, 1.5–2 mm lata; bractea inflorescentiarum plerumque minus quam 2 mm longa, nivea vel translucida; pedicellus 1.5–3 mm longus, plerumque bractea longior, gracilis, exsiccatus circa 3 mm diametro, sparsim villosus, articulatus circa in medio.

Tree ca. 5 m tall; trunk ca. 7 cm dbh; armed with simple spines below; branches and branchlets glabrate to densely strigulose or puberulent, branches arching, wide-spreading, often with straight, stout, sharp branch-spines. Petiole 2–8 mm long; blade ovate to elliptic or rarely obovate or oblanceolate, acuminate to acute or rounded at apex, obtuse to attenuate and decurrent at base, 2.5–11 cm long, 1.3–4 cm wide, glabrous to sparsely ± appressed pubescent, crenate-serrate, the teeth obscure to sharp, glandular and incurled, weakly or not at all pellucid-punctate. Stipules deltoid, 1.5–2.0 mm long. Flowers greenish-white, ca. 7 mm in diameter; in sparse, sessile, axillary fascicles; bracts usually less than 2 mm long, connate, sparsely pubescent, whitish to translucent, very thin, the outermost ± triangular, very short, the inner oval, rounded at apex; pedicels 1.5–3 mm long, slender (to 0.3 mm in diameter when dry), sparsely villous, articulate at about the middle, usually longer than bracts; calyx 3–3.5(5.5) mm long, the lobes free to the base, strigulose outside, blunt to rounded at apex, spreading at anthesis; stamens 7 or 8(9), ca. 4 mm long, erect at anthesis, fused into a ring at the base, alternating with densely villous staminodia, the staminal tube glabrous outside, pubescent inside, filaments ± glabrous, anthers ca. 1 mm long, introrse, equalling height of style, pollen yellowish, ± tacky; ovary sparsely villous, narrowly ovate; style short; stigma globular, viscid, short-puberulent. Capsule 3-valved, round to ellipsoid, to ca. 1 cm long, pale green to white, often marked with purple, the valves maroon within, marked with prominent white spots; seeds of irregular shapes, ca. 4 mm long, enveloped in a pale orange aril.

TYPE: PANAMA. CANAL ZONE: Barro Colorado Island, Armour Trail 685, *Croat 14057* (MO 2059605, holotype; DUKE, F, NY, PMA, VEN, isotypes).

Casearia guianensis var. *rafflesioides* is frequent in the understory of tropical moist forest on Barro Colorado Island and elsewhere in the Canal Zone and adjacent Panamá Province. It is also known from Darién Province. It flowers in March and April with fruits maturing from April to June.

The name *rafflesioides* refers to the fact that these plants serve as host plants for the parasite *Apodanthes casearíae* Poit. (Rafflesiaceae). The parasites flower during August and September, and at that time they can be found along the trunks of both var. *rafflesioides* and var. *guianensis*.

Additional specimens examined: PANAMA. CANAL ZONE: Barro Colorado Island, *Croat 7728, 7768, 8691, 9263, 9442, 9502, 11777, 11955, 13268* (all MO), *14869* (F, MO, NY, PMA, RSA). Near Summit Hills Golf Course, *Croat 10956A* (MO). DARIÉN: Hydro Camp Pico Pendejo, in monsoon rain forest on Río Sabana, 50 ft, *Duke 15432* (MO). PANAMÁ: Vic. of Madden Lake, *Gentry 5055* (MO).

2. **Casearia guianensis** (Aubl.) Urban var. **guianensis**—FIG. 4.

This taxon has been adequately described in the *Flora of Panama* (Robyns, 1968) and its description will not be given here. This variety is much more abundant than the other two varieties in Panama. It is known from drier parts of

3
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1
2

tropical moist forest (Holdridge, 1967) in the Canal Zone, and in the Provinces of Panama, Darien, Veraguas and Herrera. It is also known from premontane moist forest in Panamá Province. Plants flower mostly in March and April, rarely as early as January or as late as May. Fruits mature between March and June. It is phenologically similar to var. *rafflesioides* but is apparently now isolated phenologically from var. *stjohnii*. While plants generally lack branch-spines, a specimen from Mexico in Tuxpeña, Campeche (*Lundell 986*) has some branch-spines.

3. **Casearia guianensis** (Aubl.) Urban var. **stjohnii** (Johnston) Croat, comb. nov.

Casearia stjohnii Johnston, Sargentia 8: 213. 1949.

The discovery of the var. *rafflesioides* and the consequent thorough study of the variation of *C. guianensis* have made it clear that *C. stjohnii* is also only infraspecifically distinct from *C. guianensis*. The preceding combination is therefore made. Study of recently acquired specimens allows a more accurate description of the taxon:

Tree or large shrub 3–12 m tall; branches glabrous in age, sometimes with stout, sharp branch-spines, 1–3.5 cm long. Leaves mature at time of flowering, usually drying dark; petioles slender, 5–15 mm long; blade obovate to obovate-elliptic, rounded to obtuse and abruptly acuminate at apex, (the acumen blunt or sometimes absent with apex of blade rounded), acute to attenuate (sometimes obtuse) at base, 6–12 cm long, 3–6.5 cm wide, pellucid-punctate, the margin crenate, the upper surface (at least on veins) inconspicuously appressed-pubescent. Flowers greenish-yellow or greenish-white; in very dense, sessile, axillary fascicles; pedicels stout, 1–2 mm long, 0.5–0.7 mm in diameter, densely tomentose to sericeous, articulated at the middle, the stout lower half persisting; bracts oval, acute at apex, 2–3 mm long, glabrous inside, densely tomentulose outside on those surfaces exposed in bud, exceeding and obscuring the pedicels, persistent; buds subglobose; calyx 4–5.5 mm long, the lobes ovate-oblong to oblong, unequal in width, 1–1.5 mm wide, free to very near the base, densely and minutely appressed-pubescent outside, glabrous to sparsely strigulose inside in upper half; stamens 8(9), the filaments glabrous, filiform, mostly 2.5 mm long, united into a tube with alternating staminodia; anthers ca. 0.5 mm long, staminodia to 2 mm long, the free part densely villous, staminal tube nearly glabrous outside, sparsely pubescent inside, to 1 mm long; ovary narrowly ovoid, gradually tapered onto style, pilose; stigma conical-capitate, weakly puberulent, held at the level of the anthers; capsules globose to depressed-globose, green to purplish, ca. 8 mm in diameter, sparsely pubescent, apex with an old persistent style base, the 3 valves sometimes unequal, to 12 mm long and 7 mm wide after dehiscence.

←

FIGURES 1–4. *Casearia guianensis* (Aubl.) Urban.—1. Var. *rafflesioides*, showing branch-spines and flower buds (×¾).—2. Var. *rafflesioides*, fruits (×1).—3. Var. *rafflesioides*, flowers (×½).—4. Var. *guianensis*, showing precocious flowering (×½).

Known from tropical moist forest in the Canal Zone, San José Island (Panamá Province) as well as from the Provinces of Herrera and Veraguas in western Panama; also known from premontane moist forest in Los Santos Province and premontane wet forest in Chiriquí Province. Flowers in June and July. Fruits mature during August and September.

Casearia guianensis var. *stjohnii* has a perianth very similar to var. *guianensis* and var. *rafflesioides*, but has much stouter, densely tomentose pedicels and thicker, longer inflorescence bracts. The larger bracts generally hide the pedicels. This may be true even in fruit.

Perhaps the most important distinction in this variety is its different phenological behavior since plants flower and fruit later than those of vars. *guianensis* and *rafflesioides*.

PANAMA. CANAL ZONE: Vic. of Ft. Kobbe Beach, *Duke 4252* (MO). Chiriquí: Tolé, vic. of Santa Ana Well, ca. 1,000 ft, *Dwyer & Kirkbride 7456* (COL, MO, US). HERRERA: Ocú, *Ebinger 1096* (MO). LOS SANTOS: Los Asientos, *C. Wendehake 36* (MO, PMA). PANAMÁ: San José Island, *Erlanson 369* (NY, US, Type of *C. stjohnii*). VERAGUAS: ca. 5 mi N of Santiago, vic. of Santa María River, *Blum & Tyson 618* (MO).

XYLOSMA Forst. f.

Xylosma sylvicola Standley, Publ. Field Columbian Mus., Bot. Ser. 4: 316. 1929. —FIGS. 5–6.

Dioecious tree to 6 m tall, often branching near ground; trunk unarmed or rarely with branched spines; the larger branches sparsely armed with a few simple spines to 1 cm long; stems glabrous. Leaves thin; petioles ca. 5 mm long, glabrous to pubescent; blades elliptic, acuminate, acute to obtuse at base, 3–16 cm long, (1.5)3.5–7.5 cm wide, with minute, gland-tipped teeth, glabrous except sometimes puberulent on midrib below; estipulate. Flowers in very short racemes, often appearing glomerulate, inconspicuously bracteate at base; rachis 2–6 mm long; pedicels 5–8 mm long, puberulent, subtended by triangular bracts to 2 mm long; calyx deeply lobed, to 1.3 mm long, the lobes ovate, rounded at apex with margins ciliate, glabrous outside, weakly pubescent and weakly keeled inside; stamens usually 10–16, to 2.7 mm long, glabrous, anthers as broad as long; disc of male flowers 9–12-lobed, the lobes rounded, irregular; disc of female flowers entire or 2-parted; ovary ellipsoid to obovoid, ca. 1.5 mm long; style with 2 short flattened branches, each with rounded lobes. Fruits ellipsoid to obovoid, 8–12 mm long, to 9 mm wide, becoming orange, then bright red, finally violet-purple at maturity; exocarp thin; mesocarp fleshy; seeds 1–3, ovoid, ca. 5 mm long.

Ranging from Mexico (Chiapas) to Panama. Flowers seen from March to July, mostly early in the rainy season; mature fruits have been seen from April to September.

Knight 1201 has both male and female flowered twigs. If the two branches were taken from the same plant, the species is not always dioecious. Field observations showed only the dioecious condition.

This species corresponds to *Xylosma* species no. 2 in the *Flora of Panama* (Robyns, 1968). The species is best characterized by its usually thin, weakly-

FIGURES 5–6. *Xylosma sylvicola* Standley.—5. Close-up of fruits (×3¾).—6. Habit (×¾).

toothed, elliptic blades; the stout short, simple spines borne sparsely on the larger branches; very short, racemose inflorescences; dioecious plants with 9–12 stamens in the staminate flowers; and calyx lobes pubescent on the inner surface. Barro Colorado Island collections of this species differ in having larger, thinner leaves 8–16 cm long and 4–7.5 cm broad.

MEXICO. CHIAPAS: Escuintla, *Matuda 1795* (MO).
GUATEMALA. ALTA VERAPAZ: Sebol, *Contreras 4380* (F). PETÉN: Finca Yalpemech and Chinaja, 50–100 m, *Steyermark 45444* (MO).
HONDURAS. ATLANTIDA: Lancetilla Valley, near Tela, 200 m, *Standley 52917* (F, Holotype).
PANAMA. CANAL ZONE: Barro Colorado Island, *Knight 1201* (MO); *Foster 1243, 1715, 1064, 1039, 2254* (all MO, DUKE); *Croat 14640* (MO, F, NY, PMA, DUKE, K, VEN), *14642* (MO). COCLÉ: El Valle, *Dwyer 1837* (MO); *Allen & Alston 1856* (MO, F, US).

Xylosma chloranthum Donn. Sm., Bot. Gaz. (Crawfordsville) 57: 415–416. 1914.

Dioecious shrub or tree to 6 m tall; trunk usually with large, branched spines; glabrous except for puberulent young stems; stems prominently lenticellate, unarmed or armed with straight stiff axillary spines to 2.5 cm long (perhaps only on juveniles). Leaves alternate; petioles 3–5 mm long; blades narrowly-ovate to lance-elliptic, long acuminate, acute to rounded at base, 8–19 cm long, 2–6 cm wide, lacking pellucid-punctations, obtusely glandular-crenate, shiny on both surfaces, reticulate veins prominulous on both sides; estipulate. Flowers yellowish, usually occurring in leafless axils; pedicels 3–7 mm long, puberulous, articulated in lower ⅓ of male flowers and near middle of fruiting pedicel; sepals 4 or 5, very broadly ovate to nearly rounded, 1.5–2 mm long, ferruginous-puberulous and

glandular near apex, the margins ± ciliate (near apex); petals absent; stamens 22–29(35), to 6 mm long, glabrous; disc prominently undulate-lobed, style (3)4- or 5-lobed, the lobes short and spreading. Bacca ellipsoid, ca. 6 mm long; seeds few, ovoid, to 4.5 mm long.

Flowers during the dry season and early rainy season, usually while plants are still devoid of their leaves. Fruits develop within a short time, often even before the leaves have been replaced.

The taxonomy of the genus *Xylosma* is among the most seriously in need of work for all of Central American plant genera. The names used here thus will remain doubtful until a complete revision of the group can be made. This taxon has been confused with *X. excelsa* Standley & L. O. Williams which differs in being much larger (13–25 m), in being polygamous and in bearing leaves at flowering time. *Xylosma chloranthum* has also been confused with *X. intermedia* (Seem.) Tr. & Pl. The latter species has polygamous flowers and has been transferred to the genus *Eichlerodendron* (Sleumer, 1934). As judged from a photograph, the type of *X. oligandrum* Donn. Sm. appears to be very similar to the type of *X. chloranthum* Donn. Sm. and may prove to be the oldest name for this taxon. It was published in 1897.

Known from Belize, Guatemala, Costa Rica, Nicaragua and Panama. In Panama known from tropical moist forest in the Canal Zone and Panamá Province, and from premontane wet forest in Colón (Santa Rita Ridge), Chiriquí (near Boquete) and Panamá (Cerro Azul) Provinces.

BELIZE. CAYO: Mountain Pine Ridge, San Augustin, *Lundell 6754* (F).

COSTA RICA. ALAJUELA: La Palma to San Ramon, 1125 m, *Brenes 4665* (F); 1050–1100 m, *Brenes 5144, 5181* (both F). Piedades beyond San Ramon, 1050 m, *Brenes 4761* (F). San Pedro to San Ramon, 1125 m, *Brenes 4668* (F); 1075 m, *Brenes 4678* (F). GUANACASTE: 6 mi S of La Cruz, *Lent 97* (F). SAN JOSÉ: 3 km E of San Isidro, *Molina, Burger & Wallenta 18323* (F). Vic. of El General, *Skutch 4077, 3080* (both US).

GUATEMALA. ALTA VERAPAZ: Cubilquitz, *Turckheim 4111* (F, US, Type). SANTA ROSA: Volcán Tecuamburro, N of Chiquimulilla, 250–500 m, *Steyermark 33137* (F).

PANAMA. CANAL ZONE: Barro Colorado Island, *Bailey & Bailey 484* (F); *Croat 11617, 10087* (both MO); *Foster 785* (MO); *Woodworth & Vestal 419* (F, MO). COLÓN: Santa Rita Ridge, *Croat 14138* (MO). PANAMÁ: Chepo to El Llano, *Tyson & Hale Smith 4125* (MO).

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A RECONSIDERATION OF *TRICHILIA CIPO* (A. JUSS.) C.DC. (MELIACEAE)

THOMAS B. CROAT[1]

ABSTRACT

Trichilia verrucosa C.DC. is considered distinct from *Trichilia cipo* (A. Juss.) C.DC. Both species are described and the differences between them are discussed. Their range and a list of specimens cited is also given.

During the course of my work with the new Barro Colorado Island Flora, a species of *Trichilia* was discovered which in some ways resembles *T. cipo* and was included with that species under the names *T. verrucosa* C.DC. and *T. steinbachii* Harms by Smith (1965) in the *Flora of Panama* treatment. On the basis of field work on Barro Colorado Island and herbarium studies, the two taxa have been clearly delimited. Table 1 contrasts the distinguishing features which separate the two species.

Trichilia verrucosa C.DC., Monogr. Phaner. 1: 695. 1878. TYPE: Based on plate in Karst., Fl. Colomb. 2: 71, *t. 136.* 1863.—FIGS. 3–4.

Moschoxylum multiflorum Karst., Fl. Colomb. 2: 71, *t. 136.* 1863. TYPE: Colombia (not seen).

T. smithii C.DC., Annuaire Conserv. Jard. Bot. Genève 10: 163. 1907. TYPE: Colombia, Magdalena, Santa Marta, *H. H. Smith 447* (G, holotype, not seen; F, MO, NY, isotypes).

T. oblanceolata Rusby, Descript. South Amer. Pl. 37. 1920. TYPE: Colombia, near Calaqualito, 1200 ft *H. Smith 447* (NY holotype; G (not seen), F, MO, isotypes).

T. crugeriana Urb., Repert. Spec. Nov. Regni Veg. 17: 158. 1921. TYPE: Trinidad, *Crueger 185* (TRIN, holotype, not seen; NY, isotype).

T. steinbachii Harms, Notizbl. Bot. Gart. Berlin-Dahlem 9: 1156. 1927. TYPE: Bolivia, *Steinbach 7364* (MO, lectotype; F, isolectotype).

T. krukovii Gleason, Phytologia 1: 106. 1934. TYPE: Brazil, Amazonas, mouth of Rio Embira, Jurua Basin, *Krukoff 4711* (NY, holotype; MO, isotype).

Dioecious tree 5–20 m tall; outer bark minutely fissured, thin (bearing short, raised horizontal lines on inner surface); inner bark reddish-brown on the outer edge, bearing impressed short horizontal lines; sap with sweet, distinctive aroma; young twigs, leaf rachises and axes of inflorescences moderately short-appressed-pubescent, glabrous in age. Leaves alternate, pinnate, mostly 8–30 cm long, essentially glabrous; petiole flat on upper surface, with marginal ribs; leaflets usually alternate, often dimorphic, full-sized leaflets usually 3–5, often with a pair of minute, aborted leaflets at the base, rarely with 7 full-sized leaflets; blades ± elliptic, acuminate, acute to obtuse at base, 6–16 cm long and 2.5–6(8) wide, the midrib usually flat above, the major lateral veins mostly 8–12 pairs, scarcely raised below, joining before the margin. Panicles solitary in upper axils, 5–17 cm long; flowers functionally unisexual, greenish, mostly 5-parted; calyx bowl-shaped, shallowly lobed, 1–2 mm long, glabrate; petals ovate, 2–3.5 mm long, usually glabrous except minutely papillate on margin; staminal tube ½–⅔ as long

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TABLE 1. Contrasting features of *Trichilia cipo* and *T. verrucosa*.

Trichilia cipo (A. Juss.) C.DC.	*Trichilia verrucosa* C.DC.
Leaflets usually 5–9	Leaflets usually 3–5
Leaflets all of approximately equal size, the lowermost leaflets persistent (Fig. 1)	Lowermost leaflets often very much reduced, deciduous in age (Fig. 3)
Upper midrib of blade sharply raised, usually also pubescent	Upper midrib of blade usually flattened or even sunken, usually glabrous
Petals mostly less than 2 mm long	Petals mostly 3 mm long
Calyx saucer-shaped	Calyx bowl-shaped
Staminal tube usually glabrous on both sides (sometimes pubescent within near apex)	Staminal tube usually pubescent on both sides (sometimes sparsely pubescent or even glabrous outside in South American specimens)
Ovary very densely pubescent throughout	Ovary densely pubescent usually only below middle
Fruits oblong to ellipsoid (Fig. 2), orange at maturity, strongly tuberculate, sparsely appressed pubescent	Fruits globose (Fig. 4), green at maturity, minutely verrucose (rarely obovoid, then smooth), glabrous or nearly so

as petals, much broader than long, moderately to sparsely pubescent outside (often glabrous outside in South America), sparsely to densely pubescent inside; anthers twice the number of petals, slender, lightly tapered toward apex, ca. 1 mm long, dehiscing along lateral margins, alternating with and ± equalling acicular lobes of the staminal tube, the latter often pubescent at least toward the base; ovary broadly ovoid, 2–3(4)-locular, 1–2 mm wide, with dense appressed white trichomes on lower half; style ± equalling ovary at anthesis; stigma capitate, inconspicuously lobed, held at about the level of the anthers. Fruits ± globose, green at maturity, weakly verrucose, 2–3 cm diameter, ± glabrous, dehiscing by 3 valves; seeds 1 or 2, covered with a shiny red aril.

Ranges from Panama to Trinidad, Guyana, Brazil, Bolivia, and Peru. In Panama it is known from tropical moist forest (Holdridge Life Zone System) on both slopes of the Canal Zone and in Colón, Los Santos, Panamá, and Darién Provinces. In Panama the species flowers from March to May. Fruits mature from August to October. According to H. H. Smith (from data on collection of *Smith 447*) "the tree is pretty common in the forest region adjoining the north coast (of Colombia) and inland to 1500–2000 ft, occurring quite close to the margin of the sea in swampy woods." He also reports that the species flowers during January and February with another flowering season in August. This bimodal flowering is not surprising since it is also known from *Trichilia cipo* in Panama.

The name *Trichilia verrucosa* C.DC. is based on a plate and description in Karsten's *Florae Colombiae*. Karsten (1863) described the species as *Moschoxylum multiflorum*. Though he cited no specimens or type locality, it must be presumed that the type locality was also in Colombia. Later in his monograph of the Meliaceae, Casmir de Candolle (1878) named the species *Trichilia verrucosa*, citing only the type description and plate in Karsten's *Florae Colombiae*. The life

size colored plate and detailed drawings of the flower and fruit parts leave little doubt that the plant is identical to that occurring in Panama. De Candolle was unable to transfer *Moschoxylum multiflorum* Karst. to *Trichilia* because the name had already been used by Casaretto (1842) based on a Brazilian species.

Trichilia steinbachii Harms, described from Bolivia, is synonymous with *T. verrucosa*. Material of *T. steinbachii* at Berlin seen by Harms for his original description was destroyed so a lectotype is designated.

Trichilia krukovii Gleason described in 1934 is probably also synonymous but that name is invalid since the name had already been used by A. C. Smith for an unrelated Brazilian species. Material matching the type of Gleason's *T. krukovii*, all collected in southwestern Brazil in the Territory of Acre and the state of Amazonas, differs from the typical *T. verrucosa* chiefly in having smooth, usually obovoid fruits and somewhat smaller leaves, the leaflets of which sometimes have a weakly raised, often pubescent, upper midrib. While further work might show these plants to be distinct from *T. verrucosa* (at least at the varietal level), it seems best for now to include them with *T. verrucosa*.

Since most of the material in herbaria belonging to this species has been misidentified or filed under synonyms, the following list of specimens is provided for its entire range.

BOLIVIA. SANTA CRUZ: Province of Sara, Buenavista, Bosgue del Fraile, 450 m, *Jose Steinbach 7364* (F, MO, Type of *Trichilia steinbachii*), *7215 bis* (MO).

BRAZIL. ACRE: Near mouth of Río Macauhan (tributary of Río Yaco), lat. 9°20′ S, long. 69° W, *Krukoff 5626* (MO). AMAZONAS: near mouth of Río Embira, *Krukoff 4711* (Type of *T. krukovii*), *5004* (both F, MO, NY). Basin of Río Demeni, vic. of Tototobí, *Prance et al. 10205* (NY). RONDONIA: Vic. of Jaru, *Forero & Wrigley 7101* (NY).

COLOMBIA. COM. GUAJIRA: Caño Seco near Carraipa, 120 m, *Haught 4378* (US). MAGDALENA: Santa Marta, near Cacagualito, 1200 ft, *Smith 447* (NY, MO, F, Type of *T. smithii*).

GUYANA. NW slopes of Kanuku Mts. in drainage of Moku-Moku Creek, 150–400 m, *A. C. Smith 3549, 3592* (both MO, NY, US). Wabuwak Kanuku Mts., 2000 ft, *Woodblock 206, 385* (both NY).

PANAMA. CANAL ZONE: Barro Colorado Island, *Croat 4936, 5153, 5354, 10230, 10755, 11121, 11711* (all MO), *6035* (MO, US); *Foster 463, 1493* (both MO, DUKE). Vic. of Río Cocolí, road K-9, *Stern et al. 30* (F, MO). COLÓN: Buenavista, 100 m, *Holdridge 6394* (MO). DARIÉN: Río Balsa, between Manene and Tusijuanda, *Duke 13573* (MO). 2–3 mi SE of El Real, *Duke 4852*. 2 mi E of Santa Fé, *Tyson et al. 4841* (MO, US). Below village of Puero, *Duke 13119* (MO). LOS SANTOS: Guayabo W of Tonosí, *Stern et al. 1892* (MO, US). PANAMÁ: Vic. of El Llano, *Duke 5825* (MO). Woods along Pan-Am. Hwy. between El Llano and Manomí, *Duke 5529* (MO). SAN BLAS: Río Chucunaque, 2–10 mi above the Cuna-Darién border, *Duke 8564* (MO).

TRINIDAD. Moruga, *Britton & Broadway 2445* (NY). Arima, *Dannouse 8327* (NY). WITHOUT EXACT LOCALITY: *Hart 1414* (US), *2374* (US); *Crueger 185* (NY, Type of *T. crugeriana*).

VENEZUELA. ANZOÁTEGUI: NE of Bergantín, 500 m, *Steyermark 61059* (F, NY). Río León by Quebrada Danta, tributary of Río Neverí, 500 m, *Steyermark 61059* (F, US). ARAGUA: Selva de Gramitas, Pargue Nacional, *Delgado 137*. BARINAS: Ticiporo Forest Reserve, *Breteler 3536* (US). BOLÍVAR: Woods bordering savanna by Río Asa, above Raudal Cotua, S of La Paragua, *Steyermark 8675* (NY, US). Around forestry camp "potreritos" in the La Paragua forestry reserve, *Blanco 680* (NY). E slopes of Cerro Coroba, 400 m, *Wurdack 355* (F, NY, US). S of La Paragua on Río Asa, above Río Cotua, *Steyermark 86759* (F, NY, US). DELTA AMACURO: E of Río Grande, ENE of Palmar near border of Bolivar State, *Blanco 403* (US). MIRANDA: Parque Nacional Guatopo, 800 m, *Steyermark 90033* (NY). MONAGAS: Along Quebrada Colorado Grande, SW of Caripe, 850–1350 m, *Steyermark 61946* (F). ZULIA: Vic.

of Perija, *Tejera 68* (US). STATE UNKNOWN: El Charol, Río Tocuyo, *Blanco 928* (NY). EXACT LOCALITY UNKNOWN: Probably Colombia or Venezuela, Tomaraz on Río Hacha? *Karsten s.n.*

Trichilia cipo (A. Juss.) C.DC. in Mart., Fl. Bras. 11(1): 214. 1878. TYPE: Guyana, ripis fluvii Kourou, Herb. Richard (P, not seen).—FIGS. 1–2.

Trichilia tuberculata (Tr. & Pl.) C.DC., Monogr. Phaner. 1: 711. 1878. TYPE: Panama, Canal Zone, Empire, *Hayes 262* (K, holotype, not seen; F, isotype).

Dioecious tree to 30 m tall and 40 cm dbh (often much shorter along the shore); bark hard, closely fissured; inner bark red; younger stems, leaf rachises and axes of inflorescences densely strigose and puberulent (in Panama) or sparsely strigose or sparsely puberulent or nearly glabrous (often in South America). Leaves alternate, imparipinnate, mostly 15–30 cm long; petiole flat on upper surface, with marginal ribs; leaflets apparently never dimorphic, usually 5–9 (rarely 3 or 10), usually alternate, ± elliptic, acuminate, obtuse-attenuate at base, 4–21 cm long and 1.5–8 cm wide, usually glabrous or minutely puberulent and/or strigose on midribs of both sides, the surface rarely strigose below. Panicles axillary (often appearing terminal), mostly 8–20 cm long; flowers functionally unisexual, white or greenish-yellow, 4–6-parted, as wide as long, with erect or appressed trichomes (at least on calyx), globular in bud; calyx saucer-shaped, the lobes acute or blunt; petals valvate, ovate, to ca. 2 mm long, glabrous or sparsely pubescent outside, glabrous within, the margins papillose-puberulent; staminal tube ⅔–¾ as long as petals, broader than long, glabrous on both sides except sometimes pubescent within near apex, anthers twice as many as petals, very narrowly ovoid, ca. 0.5 mm long, alternating with and usually longer than the narrowly acute lobes of the staminal tube; ovary broadly ovoid, densely appressed-pubescent with white trichomes throughout; style usually glabrous. Capsule ellipsoid, 11–18 mm long, orange at maturity, prominently tuberculate, the 3(4) valves folding back to expose shiny red aril; seeds 1 or 2, smooth, ellipsoid, ca. 1 cm long.

Ranges from Guatemala to Bolivia and Guyana. In Panama known from tropical moist forest in the Provinces of Bocas del Toro, Colón, San Blas, Chiriquí (Progreso), Panamá and Darién and from tropical wet forest in Colón Province (Salud). In the Canal Zone it is known principally from the Atlantic slope. The species flowers bimodally in Central Panama but principally from April to June, especially June. Fruits mature mostly during September and October, especially October. A second but smaller flowering period may occur from September to November. Fruits from this flowering period have been seen mature in June. It is not known whether the second flowering occurs each year or if it is sporadic.

Since *Trichilia cipo* and *T. verrucosa* were lumped in the *Flora of Panama*, the following list of specimens for Panama is provided for clarification.

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FIGURES 1–4. Comparison of *Trichilia cipo* (A. Juss.) C.DC. and *Trichilia verrucosa* C.DC.—1. Habit of *T. cipo*, *Croat 6047*, ×¼.—2. Mature fruit of *T. cipo*, *Croat 6033*, ×2.—3. Habit of *T. verrucosa*, *Croat 6035*, ×¼.—4. Mature fruit of *T. verrucosa*, *Croat 6035* (see centimeter scale).

2
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PANAMA. BOCAS DEL TORO: Water Valley, *von Wedel 691* (MO, US). Changuinola Valley, *Cooper & Slater 131* (US). Almirante Region, *Cooper & Slater 56* (US). CANAL ZONE: Without exact locality, *Hayes 262* (F, Type of *T. tuberculata*). Barro Colorado Island, *Aviles 114* (F); *Bailey 394* (F); *Croat 5036A, 5096, 5237, 6033, 6047, 6161, 6321, 6713, 11736, 14924, 15057A, 15100, 15561*, (all MO), *4301, 12271, 12500, 12601, 12701, 15068* (F, MO); *Dwyer 1406* (MO); *Foster 881, 885*, (both F); *Weaver & Foster 1479* (F); *Zetek 5073* (F, MO). Darién Station, *Standley 31548* (US). NW part of Canal Zone, area W of Limón Bay, *Johnston 1517* (MO). CHIRIQUÍ: Progreso, *Cooper & Slater 217* (US), *240* (US, F). Puerto Armuelles, *Woodson & Schery 902* (F, MO). Burica Peninsula, Comarca del Baru between Cañaza and Cocos, *Stern et al. 143* (F), *146* (F, MO). COLÓN: Vic. of Sardinilla, *Blum & Tyson 499* (MO). Salúd, *Lao & Holdridge 204* (MO). DARIÉN: Río Pita, 0–2 mi above tidal limit, *Duke 4804* (MO). PANAMÁ: Vic. of El Llano, *Duke 5548, 5848* (both MO). 6 mi E of Chepo on Pan-Am. Hwy, *Duke 4059, 4068* (both MO, US). Cichébre, Chepo, *Holdridge 6501* (MO). Macaple Island in Madden Lake, *Tyson 5467, 5512* (both MO). SAN BLAS: Nakka Island, *Dwyer 6879* (MO).

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ON THE GEOGRAPHICAL ORIGIN OF *LARREA DIVARICATA* (ZYGOPHYLLACEAE)[1]

JUAN H. HUNZIKER[2]

After assessing all available evidence concerning the present distribution of *Larrea divaricata* Cav., we have suggested that it reached North America from South America (Hunziker *et al.*, 1972*a*, 1972*b*). This point of view was sustained previously by Johnston (1940). Axelrod (1950) has pointed out that the present occurrence of these relict austral types in the north can be explained by trans-tropic migration in the late Cenozoic. Long-distance dispersal across the tropics may have occurred through an intermediate series of appropriate semi-arid habitats that served as "way-stations" (Raven, 1963). The latter might have arisen as a result of the expansion of the world's arid climates in the late Tertiary and early Quaternary (Axelrod, 1970; Porter, 1974).

An alternative hypothesis is that the present disjunct range of *L. divaricata* originated by the evolution of the Chihuahuan and Argentinian types from a common trans-tropic prototype, which later became extinct (Barbour, 1969).

A third hypothesis has been suggested by Turner (1972) who claims that "it is equally likely that *L. divaricata* developed as a diploid population in North America millions of years ago, and that subsequently it was established in South America through long-range dispersal." Porter (1974) believes that the genus might just as well have arisen in North America and later have been dispersed to South America.

Turner (1972: 161–162) writes that "at least one species, *L. divaricata*, is so similar to its southern hemisphere counterpart, *L. tridentata*, that some authors have considered them to be the same species." On p. 163 he states that "as yet we do not know the origin of the apparently autojunct *Larrea divaricata*. Hunziker (personal communication, this symposium) interprets his preliminary protein-band data as suggestive of a South American origin for the group as a whole. I am more cautious, for while I recognize the better development of *Larrea* (as to number of species) in South America, I am also aware that the North American element is made of diploid, tetraploid, and hexaploid populations, all of which show considerable variation, indicative of a species with some considerable tenure in the North American deserts. I suggest, therefore, that it is equally likely that *L. divaricata* developed as a diploid population in North America millions of years ago, and that subsequently it was established in South America through long-range dispersal. The fact that there are two other species of *Larrea* in South America implies little, for *L. divaricata* may be only remotely related to these."

Unfortunately, Dr. Turner has apparently overlooked the cytogenetic, taxo-

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[1] The author wishes to thank Dr. Duncan Porter for kindly making available his unpublished work on the disjunct distributions in the New World Zygophyllaceae. The reading of this unpublished work was a stimulus for further speculation.

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nomic and geographic evidence which was presented, as was his contribution, at the Symposium on "Disjunctions in Plants" (Hunziker *et al.* 1972*b*). I must point out the following errors or omissions in Dr. Turner's statements:

1. The South American taxon is *Larrea divaricata* and its northern counterpart is *L. tridentata*. In a previous paper the same mistake was made (Turner, 1969).

2. Besides bifoliolate *L. divaricata* (Sect. *Bifolium*) there are not *two* other species in South America but *three*. These are the multifoliolate *L. ameghinoi* Speg. and *L. nitida* Cav. (Sect. *Larrea*) and the bifoliolate *L. cuneifolia* Cav. (Sect. *Bifolium*) (Hunziker *et al.*, 1969; Palacios & Hunziker, 1972).

3. The cytogenetic analysis of the *L. cuneifolia* × *L. divaricata* hybrid suggests that diploid South American *L. divaricata* has a genome in common with tetraploid *L. cuneifolia*, and the former species is one or is closely related to one of the two diploid progenitors of *L. cuneifolia* (Hunziker *et al.*, 1972*a*, 1972*b*). As is indicated by the chromosome behavior of their hybrid and the morphology of both taxa (Hunziker *et al.*, 1972*a*, 1972*b*; Palacios & Hunziker, 1972), *L. divaricata* is clearly not "remotely related" to *L. cuneifolia*.

I would also like to point out several other facts that should be considered in relation to the origin of *L. divaricata*:

1. *Larrea cuneifolia* is possibly a relatively old species having a wide distribution in Argentina. The *divarcata* genome which exists in *L. cuneifolia* (see above) would, therefore, be an ancient one in South America.

2. Multifoliolate species are very likely more primitive in the Zygophyllaceae than bifoliolate species. Reduction in number of leaflets seems to be an adaptation to aridity and a specialized and derived condition (Hunziker *et al.*, 1972*a*, 1972*b*). For instance, the genus *Bulnesia*, has six multifoliolate and only one bifoliolate species. *Larrea divaricata* and *L. cuneifolia*, each with only two leaflets per leaf, would represent more recent types within the genus.

3. As pointed out by Axelrod (1950), *Larrea* belongs to a family of tropical and subtropical affinity "which suggests a long history on the margins of the tropics in austral areas, particularly at low to middle latitudes where tropical savanna and similar environments have long been in existence."

Bulnesia, a genus related to *Larrea*, is restricted to South America and apparently evolved there. It has two species in Colombia and Venezuela (north of the equator) and five with a southern distribution (Argentina, Chile, Peru and Paraguay). Six of the seven species that have been studied so far are diploids (Poggio & Hunziker, unpublished). Apparently, in *Bulnesia*, as in *Larrea*, primary speciation occurred in South America but polyploidy and long-distance migration to North America have not occurred. Both *Larrea* and *Bulnesia* are so far the only genera in the subfamily Zygophylloideae known to have $x = 13$. It would be interesting to know, among others, the basic number of *Plectrocarpa* and *Metharme*, which also are strictly South American, and *Porlieria*. The first two genera, according to Engler (1896), are so close to *Larrea* that they can be considered early derivations from an ancestral *Larrea* type. The genus *Porlieria* is now also considered to be strictly South American by Porter (1974). Porter

pointed out that "phylogenetic relationships within the Zygophyllaceae are still somewhat hazy" and that *Larrea* appears to belong with a series of poorly known, mainly monotypic, shrubby desert genera. These are, according to Porter (1974), *Metharme* (monotypic, Chile), *Neoluederitzia* (monotypic, South-West Africa), *Plectrocarpa* (2 species, Argentina). *Sericodes* (monotypic, Mexico) and *Sisyndite* (monotypic, South West Africa, South Africa). Actually, of the eight genera within the subfamily Zygophylloideae related to a greater or lesser extent to *Larrea*, only one has a strictly North American distribution (*Sericodes*). Another ranges from North to South America through the tropics (*Guaiacum*). Of the others, four have a South American distribution (*Plectrocarpa*, *Metharme*, *Bulnesia*, *Porlieria*) and two are from southwestern Africa (*Neolueredítzia*, *Sisyndite*). This supports Axelrod's idea of a long history for the family on the margin of the tropics in austral areas.

Porter (1974) thinks that *Larrea* is most similar morphologically (in terms of flowers and fruits) to *Sericodes*. The latter genus, however, has simple leaves and it should be remembered that the fruits of a primitive *Larrea* (represented today by multifoliolate forms such as *L. nitida*) may well have been puberulous and indehiscent.

Data from comparative anatomy, morphology, cytology and palynology are badly needed for all the genera related to *Larrea* in order to obtain further evidence on its origin.

I believe that in *Larrea* there has been primary speciation at the diploid level (*L. nitida*, *L. ameghinoi*, *L. divaricata* subsp. *divaricata*) with occasional hybrid speciation involving allotetraploidy (*L. cuneifolia*), both processes occurring in South America. This situation parallels that of the related genus *Bulnesia*, except for the occurrence of polyploidy.

Taking into consideration some of the above considerations and following Occam's razor principle we have suggested that *L. divaricata* in South America would be older than in North America (Hunziker *et al.*, 1972*a*, 1972*b*). In our studies we are following the proposal by Felger & Lowe (1970) by giving subspecific status to both taxa: *L. divaricata* Cav. subsp. *divaricata* for the South American taxon and subsp. *tridentata* (Sessé. & Moç. ex DC.) Felger & Lowe for the North American one. This treatment should be regarded as provisional until more experimental data on the artificial hybridization between the North and South American taxa are obtained.

Yang (1968, 1970) and Barbour (1969) have established the existence of diploid, tetraploid and hexaploid chromosomal races within *L. divaricata* subsp. *tridentata*. These races replace each other from southeast to northwest in the Chihuahuan, Sonoran and Mojave deserts, respectively. There is increase in ploidy level with increased aridity of the deserts and the present distribution of chromosomal races suggests a south to north pattern of migration from Mexico to California and Utah.

The migration of *L. divaricata* to North America and its subsequent differentiation into *L. divaricata* subsp. *tridentata* and its tetraploid and hexaploid races has been a less radical and probably more recent and rapid development than the

speciation that occurred in South America. It probably involved mere racial differentiation and interracial polyploidy as suggested by the exomorphology and our data from protein electrophoresis and chromatography of phenolic compounds (Hunziker *et al.*, 1972*a*, 1972*b*).

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NEW COMBINATIONS AND NOTES ON CENTRAL AMERICAN MARANTACEAE

HELEN KENNEDY[1] AND DAN H. NICOLSON[2]

Three new combinations are made: *Calathea inocephala*, *Stromanthe jacquinii*, and *Stromanthe guapilesensis*. Complete synonymies are given for these taxa, including evaluation of misapplications and previous usages of illegitimate epithets.

Calathea inocephala (O. Kuntze) Kennedy & Nicolson, comb. nov.

Phyllodes inocephalum O. Kuntze, Rev. Gen. Pl. 2: 694. 1891. TYPE: Matachin, [Canal Zone] Panamá, 8 June 1874, *O. Kuntze 1916* (NY! mounted on 3 sheets).

Calathea barbillana Cufodontis, Ann. Naturhist. Mus. Wien 46: 235. 1933. TYPE: In regione Atlantica in silva densa ripae sinistrae fluminis Río Barbilla, prope "Waldeck" ad viam ferream, 28 milia a Puerto Limón, ca. 70 m, Province Limón, Costa Rica, 12 May 1930, *G. Cufodontis 581* (W, destroyed; photographed by F, neg. no. 30908 and 30909!).

Calathea altissima sensu auctt. non (Poeppig & Endlicher) Koernicke: Schumann, Pflanzenr. 48: 94. 1902; Standley, Publ. Field Mus. Nat. Hist., Bot. Ser. 18: 192. 1937; Woodson & Schery, Ann. Missouri Bot. Gard. 32: 94. 1945; Standley & Steyermark, Fieldiana, Bot. 24(3): 209. 1952.

Kuntze's protologue states "*Phyllodes inocephalum* O. Ktze. n. sp. (*Calathea in.* O. Ktze. olim)." It appears that *Phyllodes inocephalum* is a new combination based on *Calathea inocephala* but, in fact, *C. inocephala* was never previously published and was only used as a herbarium name by Kuntze. The original labels of the types have had the top portions cut off and the name *Phyllodes inocephalum* written on the remaining portion.

The combination *Calathea altissima*, which is based on the Amazonian *Phrynium altissimum* Poeppig & Endlicher, has been misapplied to this predominantly Central American species. In both *C. altissima* (Poeppig & Endlicher) Koernicke and *C. inocephala* the bracts are short-lived and break down with age, fraying into a mass of fibers (vascular strands), giving the inflorescence a distinctive and characteristic appearance. Because this character is quite unusual and occurs in both species, the confusion is understandable. However, in the original description of *Phrynium altissimum* Poeppig and Endlicher mention the presence of "bracteolis innumeris subulatis, rigidissimis." These bracteoles are absent in the types of *C. inocephala* and *C. barbillana*. *Calathea inocephala* is a much taller and more robust plant overall than is *C. altissima*.

The type photograph of *Calathea barbillana* agrees very well with the type of *C. inocephala*, as do specimens examined which were collected in the vicinity of the type locality. This is the only known species of *Calathea* in Central America in which the bracts dilacerate into fibers.

Stromanthe jacquinii (Roemer & Schultes) Kennedy & Nicolson, comb. nov.

Maranta lutea Jacquin, Ic. Rar. 2: 1, *t. 201*, 1789, Collect. 4: 117. 1791, non Aublet, 1775. TYPE: Crescit in sylvis udis ad Caracas (cited in Collect.).

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Maranta jacquinii Roemer & Schultes, Systema 1: 558. 1817. TYPE: *Maranta lutea* Jacquin (1789), non Aublet (1775).
Phrynium luteum Sweet, Hort. Brit. 2: 494. 1830, (nom. illegit., incl. *M. jacquinii* in synonymy).
Thalia lutea Steudner, Index Sem. Hort. Berol. (App.): 10. 1857, (nom. illegit., incl. *M. jacquinii* in synonymy).
Marantopsis lutea Koernicke, Bull. Soc. Imp. Naturalistes Moscou 35: 97. 1862, (nom. illegit., incl. *M. jacquinii* in synonymy).
Stromanthe lutea Eichler, Abh. Akad. Berlin 1883: 81. 1884, (nom. illegit., incl. the type of *M. jacquinii* which is included by citation of *M. lutea* Jacquin); Woodson & Schery, Ann. Missouri Bot. Gard. 32: 104. 1945.
Hymenocharis jacquinii (Roemer & Schultes) O. Kuntze, Rev. Gen. Pl. 2: 691. 1891, (based on *Maranta jacquinii*, which O. Kuntze wrongly attributes to Presl).
Myrosma lutea Macbride, Field Mus. Nat. Hist., Bot. Ser. 11: 59. 1931, (nom. illegit., incl. the type of *M. jacquinii* which is included by citation of *M. lutea* Jacquin).

Maranta lutea Jacquin (1789) is illegitimate as a later homonym of *Maranta lutea* Aublet (1775) (Art. 64, Stafleu *et al.*, 1972). Roemer and Schultes, noting Jacquin's error, renamed Jacquin's taxon *Maranta jacquinii*. All subsequent binomials ending in *lutea* are illegitimate (nomenclaturally superfluous) because all authors cited in synonymy or included the type of *Maranta jacquinii* Roemer & Schultes, the earliest available epithet that ought to have been adopted (Art. 63, Stafleu *et al.*, 1972).

Schumann (1902: 48) included *Maranta juncea* Noronha (Ver. Batav. Genootsch. 5: 20. 1790) in synonymy of *Stromanthe lutea*. Noronha doesn't appear to be describing a new taxon but attributes the binomial to Lamarck (1786), a taxon now known as *Ischnosiphon arouma* (Aublet) Koernicke.

Stromanthe guapilesensis (Donnell Smith) Kennedy & Nicolson, comb. nov.

Myrosma guapilesensis Donnell Smith, Bot. Gaz. (Crawfordsville) 23: 251. 1897 '*guapilesense*'.

Woodson & Schery (1945: 104) and Standley & Steyermark (1952: 219) cite *Myrosma guapilesensis* Donnell Smith in synonymy of *Stromanthe lutea* Eichler.

The taxon, *Myrosma guapilesensis*, falls in *Stromanthe* by virtue of its deciduous bracts, antitropic leaves, larger and branching habit, branching inflorescence and the relatively long-petiolate leaf subtending the inflorescence. It is distinct from *Stromanthe jacquinii* by virtue of its sulcate ovary (and capsule), basal leaves, and having at least two pairs of flowers per bract, while *S. jacquinii* has a smooth ovary (and capsule), leaves predominantly clustered above an elongate internode and with only a single pair of flowers per bract. *Stromanthe guapilesensis* is known only from the Atlantic slope of Costa Rica. *Stromanthe jacquinii* is known only from central Panamá just north of the Canal Zone (Cerro Campana) south into Colombia and Venezuela.

Linnaeus filius (1781: 8, 80) established *Myrosma*. This is apparently a compound word uniting two names, μυρον (*myrŏn*, n., perfume) and ὀσμη (*ŏsmē*, f., smell), yielding a feminine word meaning "perfume-smell." A few earlier authors, including John Donnell Smith, erroneously treated this feminine generic name in neuter, for example, *Myrosma guapilesense* Donnell Smith. This error is to be corrected under Art 23, paragraph 5 and Rec. 75(2) (Stafleu, *et al.* 1972).

We specifically exclude *Stromanthe lutea* sensu Standley & Steyermark (1952:

219, fig. 41) from the synonymy of both S. *jacquinii* and S. *guapilesensis*. although Standley and Steyermark called this taxon *Stromanthe lutea* and included *Myrosma guapilesensis* in synonymy. Their Guatemalan to Honduran taxon is *Stromanthe hjalmarssonii* (Koernicke) Petersen, which is distinguished by its villous leaf-sheaths, petioles and inflorescence and particularly by its densely villous ovary.

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THE GENUS *WITTMACKANTHUS* (RUBIACEAE)

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ABSTRACT

The name *Wittmackanthus* is accepted as the correct generic name for *Pallasia* Klotzsch, a later homonym. Assignment of the genus to tribe Cinchoneae, next to *Calycophyllum*, is supported by the combination of vertically imbricate ovules and alate seeds. Previous authors assigned the genus to tribe Rondeletieae, having misinterpreted the placement of the ovules and seeds as horizontal and both as exalate. One species is recognized, *W. stanleyanus*, occurring in Panama, Colombia and Guyana, and its variability is discussed.

One of the most beautiful of Rubiaceae was described in 1844 by Robert Schomburgk from the Rupununi River region of Guyana as *Calycophyllum stanleyanum*. This tree is noteworthy in having one or occasionally two calyx lobes of some flowers expanded into a conspicuous, petaloid, roseate appendage, and is of striking appearance when covered with hundreds of these brightly colored structures.

Several years ago Dr. Lorenzo Uribe Uribe (COL) sent specimens collected in the Department of Santander, Colombia, of a tree which the senior author identified as *Pallasia stanleyana* (Schomb.) Klotzsch, presumed conspecific with the tree from Guyana. Upon comparison with other collections, it became apparent that the taxon, *Pallasia stanleyana*, was in need of critical study, especially from the standpoint of its tribal position within Rubiaceae.

HISTORY OF THE GENUS

Calycophyllum stanleyanum was based upon specimens collected in one of the valleys of the Rupununi River of Guyana, at approximately lat. 3° 55′ N, long. 59° 15′ W. Klotzsch (1853) without explanation erected the genus *Pallasia* for Schomburgk's taxon. Unfortunately, *Pallasia* Klotzsch is a later homonym, previously having been proposed for four different taxa (see generic synonymy). Walpers (1858), Bentham & Hooker (1873), Schumann (1889, 1891), and Dalla Torre & Harms (1900–1907) have employed the generic name *Pallasia* Klotzsch, and the name was proposed for conservation by Mansfeld (1935), but his proposal was never adopted. The next available name for *Pallasia* Klotzsch is *Wittmackanthus* O. Kuntze (1891). Standley (1930) did not include the genus in his Rubiaceae of Colombia, as no Colombian material was known to him at the time.

MORPHOLOGY AND TRIBAL AFFINITY

In the protologue of *Calycophyllum stanleyanum* no mention was made concerning the position of the ovules, whether vertical or horizontal to the placenta. Klotzsch (1853), followed by later authors, described the ovules and seeds as

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"exalate." Bentham & Hooker (1873) described the seeds as horizontal. Schumann (1889) followed Klotzsch (1853) and Walpers (1858), except that he stressed the position of the ovules as "horizontaliter affixa," stating, however, "capsula et semina non visa."

Our study indicates that the placement of *Wittmackanthus* (*Pallasia* Klotzsch) in tribe Rondeletieae is erroneous due to the misinterpretation of the placentation and to the mistaken idea that the ovules and seeds are exalate. In fact, the ovules, as well as the seeds, are vertically adnate to the placenta and definitely winged, and the ovule body is flattened, peltately attached, and, together with the wing, appressed parallel to the thickish fleshy placenta. The vertically imbricate ovules and winged seeds place *Wittmackanthus* within tribe Cinchoneae, not in tribe Rondeletieae which has horizontal ovules and mostly seeds not winged. These criteria distinguishing tribe Cinchoneae from Rondeletieae have been accepted by most students of Rubiaceae, including Verdcourt (1958) and Bremekamp (1965).

In the protologue, Schomburgk stated, "stamina et ovarium omnino Calycophylli," and failed to note any irregularity of the corolla or of the stamens. However, starting with Klotzsch (1853) who was followed by Walpers (1858), the corolla was described as "incurva" and the stamens as "inaequilonga." In his treatment of the Rubiaceae in *Die Natürlichen Pflanzenfamilien*, Schumann (1891) employs the curvature of the corolla as one of the characters differentiating *Pallasia* from *Warszewiczia*, and in his treatment of the family in Martius's *Flora Brasiliensis*, he (Schumann, 1889) states that the corolla is "leviter sursum curvata." Actually, such a curvature does not appear to exist, or at best is so inconspicuous that it is easily passed over. Examination of corollas from various collections indicates that while the unequally inserted stamens and somewhat unequal corolla lobes lend a slight asymmetry to the corolla, there is scarcely any curvature, the corolla tube presenting a straight or nearly straight appearance.

Generic Status

The closest relative of *Wittmackanthus*, as realized by Schomburgk, is *Calycophyllum*. The differences between the two genera are in the stamens and inflorescences. The stamens of *Calycophyllum* are equal and exserted and its inflorescences are cymose or corymbiform. In contrast, the stamens of *Wittmackanthus* are unequal and included, while its inflorescences are spicate.

Variation

A study of *W. stanleyanus* shows variation in: a) length and shape of the foliaceous appendage of the calyx lobe, b) length of corolla tube and lobes, c) pubescence of the throat and outer surface of the corolla tube, d) size and apex of leaf-blades, and e) variation of pubescence on the lower surface of the leaf-blades. It was at first believed that two taxa were involved. The Panamanian plant known as *Rondeletia dukei* differed from the Colombian material collected by Uribe in having the foliaceous appendage not only cuneate at base, instead of broadly rounded to subtruncate, but also smaller (1–3.5 cm instead of 4–7 cm

long), the corolla tube shorter (8 mm or less instead of 9–9.5 mm long), the corolla lobes shorter (2–3 mm instead of 4–4.5 mm long), the leaf-blades smaller (5.5–10 × 3.5–6 cm instead of 12–15 × 6–9 cm) with the apical portion obtuse instead of acuminate, and, finally, in having the lower face of the leaf-blades ciliate in the nerve axils instead of pilosulous with spreading hairs along the midrib and lateral nerves. However, other Colombian material is intermediate. For example, in *Haught 4621*, the blade of the foliaceous appendage is 2.5–4 cm long, while that of *Cavender s.n.* is 3.5 cm, and that of *Fosberg 21922* varies from 3 to 6 cm. The length of the corolla, likewise, varies, being 6–7 mm long in *Haught 4621*. The leaves of the Schomburgk collections from Guyana were described as "utrinque glabriusculis," but these same specimens are described by Schumann (1889) as "subtus ad axillas nervorum puberulis ceterum glaberrimis." Schomburgk's collection at NY has a few short hairs along the midrib of the dorsal face of the leaf-blade, whereas in *Haught 4621* and *Fosberg 21922* tufts of hairs appear in the nerve axils or along the secondary nerves where they emerge from the midrib. In the type collection of *Rondeletia dukei* (*Duke 8329*), the hairs along the lower midrib and at its junction with the lateral nerves are denser. Hairs on the peduncles vary from 0.01 mm in *Duke 8329* to 0.02 mm in *Haught 4621*, 0.07 mm long in *Fosberg 21922*, and 0.12 mm long in *Cavender s.n.* While most of the specimens examined have the leaf-blades acuminate at apex, the type collection of *W. stanleyanus* (*Schomburgk 356/411 B* at K) has leaves varying from acute to obtuse or even rounded at apex, even though Schomburgk (1844: 623) originally described them as "acutissimae." The type collection of *R. dukei* from Panama has blades obtuse to rounded at apex, but may have been collected from an abnormal plant. Finally, the size of leaf-blades is quite variable and has no taxonomic significance.

TAXONOMIC TREATMENT

Wittmackanthus O. Kuntze, Rev. Gen. Pl. 1: 302. 1891. TYPE: *W. stanleyanus* (Schomb.) O. Kuntze.

Pallasia Klotzsch, Monatsber. Akad. Wiss. Berlin 498. 1853; not *Pallasia* Houtt., Handl. II: 382. 1775, Cucurbitaceae; not *Pallasia* Scop., Introd. 72. 1777, Gramineae; not *Pallasia* L. f., Suppl. 37. 1781, Polygonaceae; nor *Pallasia* L'Her. ex Ait., Hort. Kew. III: 498. 1789, Compositae.

Trees or shrubs. Leaves opposite, crowded near apices of the branches, petiolate. Stipules interpetiolar, ± persistent. Inflorescence terminal and axillary, spicate. Flowers subzygomorphic, 4–6-merous. Calyx cupular, deeply 4–6-fid, the lobes persistent to deciduous. Corolla tubular, straight or nearly so, the lobes imbricate in aestivation. Stamens unequal, 3 often included and 2 slightly exserted, attached to the upper part of corolla tube; anthers versatile, sagittate at base; pollen 3-colpate, smooth. Disc cupulate. Stigma sub-bilobate. Ovary bilocular; ovules ∞, anatropous, vertically imbricate and adnate to the fleshy elongated placenta, narrowly winged. Capsule septicidally dehiscent, crowned by the calyx. Seeds vertically imbricate, narrowly winged. Embryo, very small, embedded in a fleshy albumen; cotyledons ovate, obtuse; radicle cylindrical.

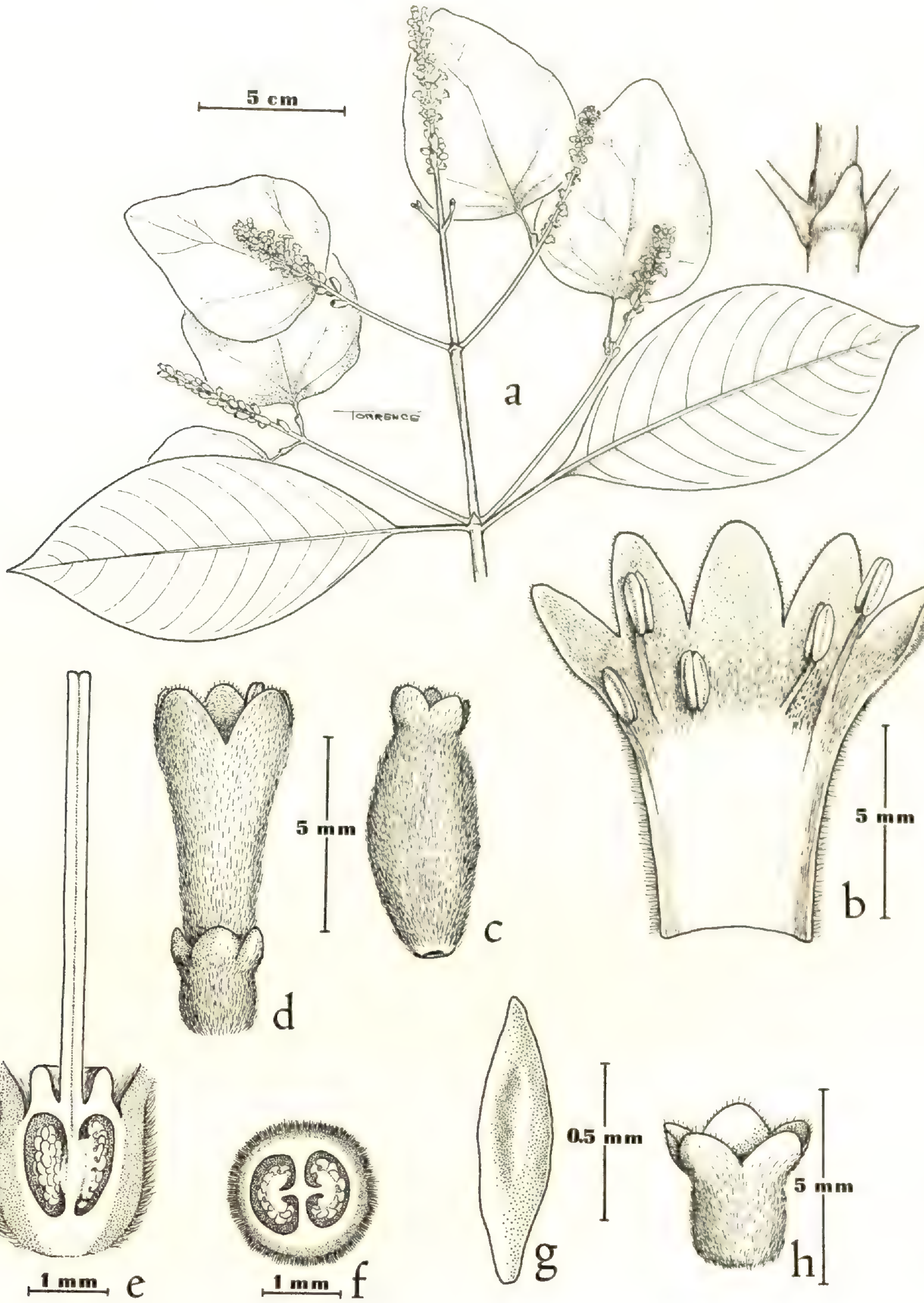

FIGURE 1. *Wittmackanthus stanleyanus*.—a. Habit of flowering branch.—b. Corolla; internal view showing unequal stamens.—c. Capsule.—d. Corolla with calyx and hypanthium.—e. Vertical section through ovary.—f. Transverse section through ovary.—g. Seed.—h. Calyx and hypanthium.

Wittmackanthus stanleyanus (Schomb.) O. Kuntze, Rev. Gen. 1: 302. 1891.—FIG. 1.

Calycophyllum stanleyanum Schomb., Jour. Bot. (Hooker) 3: 622, *t. 23, 24.* 1844.
Pallasia stanleyana (Schomb.) Klotzsch, Monatsber. Akad. Wiss. Berlin. 498. 1853; Walper, 1858, p. 122; Bentham & Hooker, 1873, p. 48; Schumann, 1891, p. 36; Schumann, 1889, p. 219; Dalla Torre & Harms, 1907, no. 8176; Mansfeld, 1935, p. 443.
Rondeletia dukei Dwyer & Hayden, Ann. Missouri Bot. Gard. 54: 144, *fig. 4.* 1967.

Trees or shrubs, 4–15 m tall, the young stems puberulent to glabrous. Stipules erect-appressed, triangular-ovate, obtuse to subacute, 3.5–6 mm long and 2–4 mm wide, glabrous or puberulous along margins and apex. Leaf-blades firmly membranous, oblong- or ovate-elliptic or obovate, acute or acuminate to obtuse or rounded at apex, cuneately acute at base, 4–17 cm long and 3–9.5 cm wide, glabrous above, glabrous below except along midrib or in axils, and/or along some lateral nerves near their junction with midrib where spreading-pilose; lateral nerves 8–15 each side, curved-ascending, inconspicuously anastomosing 1–4 mm from margin, impressed above, slightly elevated below; tertiary venation manifestly reticulate, conspicuous on both sides. Petioles 1–5 cm long, canaliculate and marginally puberulous above, otherwise sparsely puberulent to glabrous. Inflorescence of terminal or axillary pedunculate spikes, usually trichotomous or only the central spike developed; peduncles 2.5–8 cm long, ± puberulent with the hairs 0.01–0.12 mm long; rachis of spikes erect, closely many-flowered, 2.5–9 cm long, 0.5–2 cm in diameter. Flowers alternate to subverticillate, sessile or the lowest shortly pedicellate, subtended by an outer larger bract and two smaller bracteoles. Bract deciduous, ovate to oblong-lanceolate, acute, 1.5–4 mm long and 1–1.5 mm wide, puberulous without; bracteoles paired, deciduous in fruit, suborbicular to ovate-oblong, rounded or subtruncate, 0.5–1.5 mm long and 0.7–1.5 mm wide, puberulous without and ciliolate. One, rarely 2 calyx lobes of some lower flowers expanded into a showy clawed blade, the claw 2–5 mm long, pilosulous, the blade membranous, pink, purplish-pink, or rose-lilac, suborbicular-ovate to broadly ovate, obtuse to rounded at apex, broadly rounded or subtruncate to cuneately subacute at base, 1–7 cm long and 1.8–6 cm wide, 5–7-plinerved, the tertiary veins laxly and grossly reticulate, the secondary nerves together with the midnerve puberulous, elsewhere glabrous to glabrate on both surfaces. Calyx of the other flowers deeply 4–6-fid, the lobes subpersistent to caducous, suborbicular to broadly ovate or oblong, rounded to obtuse at apex, 1.4–2 mm long and 1–2 mm wide, villosulous without, glabrous within. Hypanthium narrowly oblong to urceolate, 1.5–2 mm long and 1.5–2 mm wide, longer than the bracteoles, densely buff- to cinereous-sericeous. Disc shallowly repand-lobulate, 0.4 mm high, 1 mm in diameter. Corolla purplish, 8–13.5 mm long, the tube 6–9.5 mm long, 1.7 mm wide at base, 3 mm wide at orifice, densely hirtellous to substrigose without, glabrous within except densely pilosulous to sparsely puberulent at orifice and near summit. Anthers narrowly oblong, 0.8–1.5 mm long; filaments 0.3–3 mm long, glabrous. Style 6–9 mm long, glabrous, slightly exserted beyond orifice. Ovules oblong to subelliptic-oblong. Capsule (immature) narrowly oblong to oblong-turbinate, 4–10 mm long and 2.5–4 mm wide, densely appressed-pubescent to hirsutulous. Seeds pale brown, narrowly fusiform, 0.8–0.9 mm long and 0.1 mm wide.

Distribution: Wet forests at low altitudes (60–200 m), of Panama, Colombia and Guyana.

Specimens examined: PANAMA. DARIÉN: Río Pirre, *Duke 8329* (NY, isotype of *Rondeletia dukei*).

GUYANA. "Roraima," *Rob. Schomburgk 356/411 B* (K, photo of type collection of *Calycophyllum stanleyanum*; NY, isotype).

COLOMBIA. ANTIOQUIA: Near Guapá, 53 km S of Turbo, 60 m, *Haught 4621* (COL, NY). Near Medellín, *Cavender s.n.* (NY). BOLÍVAR: Lands of Loba, Amargamiento Rico, *Curran 62* (F). Palotal, *Romero-Castañeda 1672* (COL, F), *1691* (COL). SANTANDER: Barrancabermeja, 200 m, *Uribe Uribe 6648* (VEN). Valle del Río Magdalena, *Uribe Uribe & Rojas 6300* (VEN), *Uribe Uribe 3042* (COL). 4 km E of Puerto Olaya, 150 m, *Fosberg 21922* (NY). WITHOUT LOCALITY: *Schiefer 747* (COL, F); *Montenegro 1691* (COL); *García-Barriga 13442* (COL); *Flor Claes 865* (BR, photo NY).

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NOTES

NEW COMBINATIONS IN THE GENUS *HAUYA* (ONAGRACEAE)

The following new combinations are published in advance of our monograph of *Hauya* in order to make them available for use in other publications. For reasons that will be explained in detail in the monograph, we recognize only two species, *H. heydeana* Donn. Sm. and *H. elegans* DC., the latter consisting of the following three subspecies in addition to the nominate one:

Hauya elegans DC. subsp. **barcenae** (Hemsley) Raven & Breedlove, comb. nov.

Hauya barcenae Hemsley, Diagn. Pl. Nov. 1: 13. 1878.

Hauya elegans DC. subsp. **cornuta** (Hemsley) Raven & Breedlove, comb. nov.

Hauya cornuta Hemsley, Diagn. Pl. Nov. 1: 13. 1878.

Hauya elegans DC. subsp. **lucida** (Donn. Sm. & Rose) Raven & Breedlove, comb. nov.

Hauya lucida Donn. Sm. & Rose, Bot. Gaz. (Crawfordsville) 52: 48. 1911.

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A NEW *MORMODES* (ORCHIDACEAE) FROM PANAMA

Among the specimens of *Mormodes* (Orchidaceae) received from Dr. Robert L. Dressler who collected them in Panama, a new species was found which I propose with the following description.

Mormodes lancilabris Pabst, sp. nov.—Fig. 1.

Epiphytica, *radicibus* crassis, cinereis; *rhizomate* valde abbreviato; *pseudobulbis* cylindraceis, abrupte acutis; *foliis* in plantis floriferis absentibus; *inflorescentia* erecto-patula, 40 cm alta, dimidio superiore laxe 6-flora; *floribus* patentibus, flavo-viridibus cum labello eburneo; *sepalis* lanceolatis, sepalis lateralibus paulo assimetricis, 3.5 cm longis, 8 mm latis, sepalo dorsale 7 mm lato; *petalis* anguste lanceolatis, paulo falcatis, 3.3 cm longis, 10 mm latis; *labello* lanceolato, breve unguiculato, apice acuminatissimo, 3 cm longo, 1.7 cm lato, tertia parte superiore fovea anguste-elliptica cum fovea basali, laneolata connexa donato; *columna*

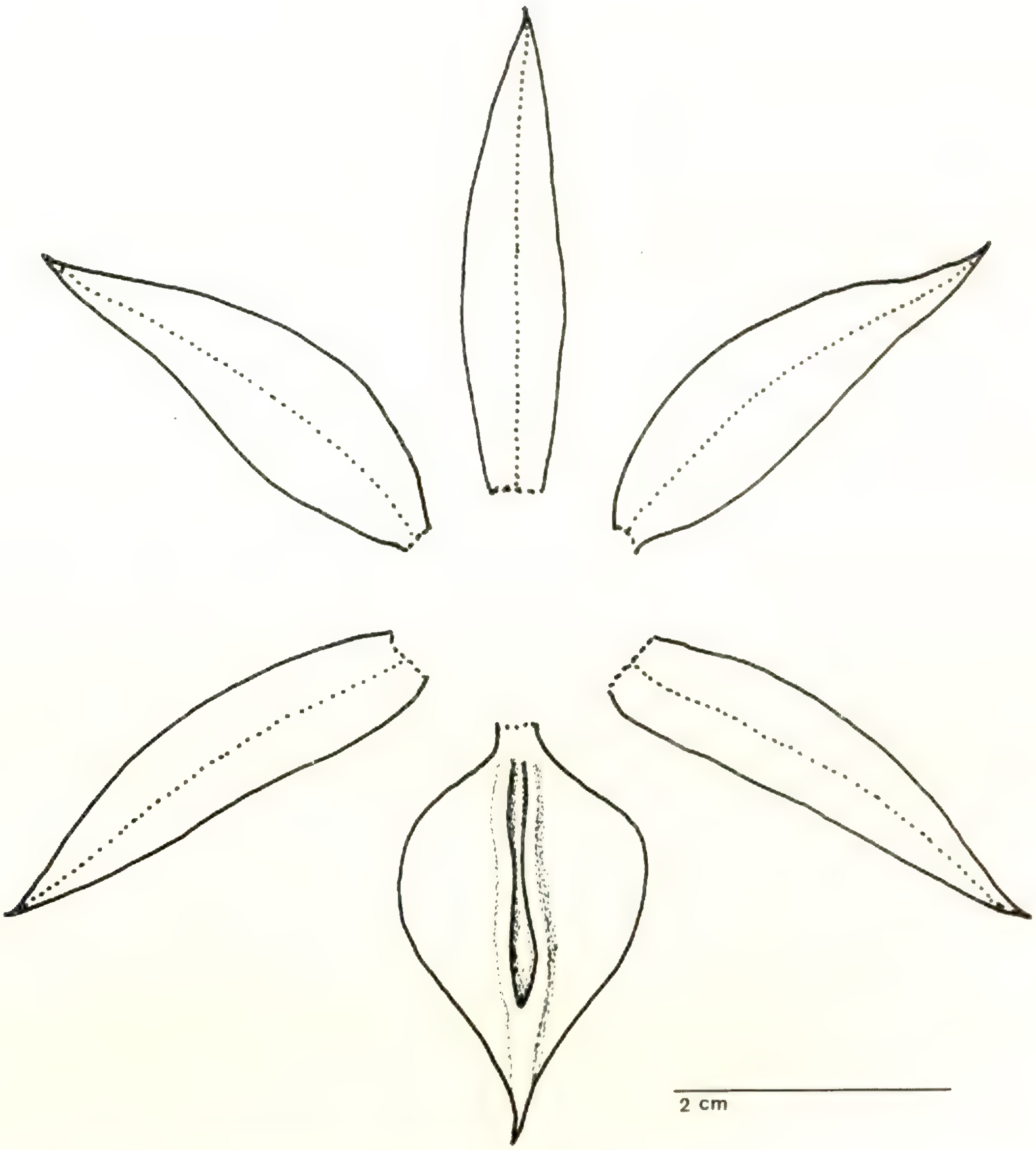

FIGURE 1. Perianth of *Mormodes lancilabris* Pabst.

contorta, gracili, semi-tereti, apice longe rostrata; *ovario* cum pedicello 3.5 cm longo.

TYPE: PANAMA. COCLÉ: Atlantic side of El Valle de Antón, floruit in cultura, 22 Nov 1965, *R. Dressler s.n.* (HB, holotypus).

Related to *Mormodes colossus* Rchb. f. and *M. powellii* Schltr. and characterized by the lanciform lip, this new species is distinguished by the shape of the lip, which is very regularly ovate-acute and differently proportioned, beside the greenish-yellow flowers with ivory lip.—*G. F. J. Pabst, Herbarium Brandeanum, Rio de Janeiro, Brasil.*

PRIORITY OF *LECYTHIS AMPLA* MIERS OVER *L. COSTARICENSIS* PITTIER

One of the conspicuous trees of premontane wet and tropical wet forest of lower Central America and northwestern Colombia is *Lecythis ampla*. This magnificent tree, reaching 30–40 m in height, is easily recognized by its chocolate brown, longitudinally furrowed bark, buttressed trunk, small leaves and large fruits (usually present in various stages of decomposition under the tree).

Lecythis ampla ranges from the lower Magdalena Valley of Colombia, throughout the Darién of Panama, along the Atlantic coasts of Panama and Costa Rica, and reaches the northern limits of its range in the plains of southeastern Nicaragua. Altitudinally it is distributed from near sea level (Puerto Obaldia, Panama; Sarapiqui Valley, Costa Rica; southeastern Nicaragua) to 800 m (Cerros Tacarcuna and Pirre in Darién, Panama).

Although the fruits of the species display considerable variation in absolute size, size of opercular opening and position of calyx scar, this variability does not merit specific recogniton. As has been discussed by Dugand (1947) for *L. minor* Jacq. and Mori (1971) for *L. ampla*, such variation is to be expected within populations and even in the same individual of *Lecythis* species. Pittier's (1908: pl. 7) photograph of fruits of the type of *L. costaricensis* (= *L. ampla*) also illustrates variation in this species. However, he later (Pittier, 1927) described *L. armiliensis* from a single fruit that clearly falls within the range of variation so well illustrated for his *L. costaricensis*.

My field observations of this species in Nicaragua, Costa Rica, Panama and Colombia support the conclusion that all small-leaved, large-fruited individuals of *Lecythis* from this region belong to the same species. Any attempt to taxonomically recognize fruit variation would result in a plethora of names completely unrelated to the biology of the species.

The most commonly applied name for this taxon has been *L. costaricensis*. Much earlier John Miers (1874) described and illustrated *L. ampullaria* and *L. ampla* from Antioquia, Colombia. Both species were based solely on fruits and seeds—the former on a fruit which had been altered by man to form a "water bottle" (cf. Miers, 1874: fig. 38) and the latter on an unaltered fruit and seeds of dubious origin. Nonetheless, the drawings and fruit descriptions are enough to identify both fruits with the species under consideration.

Although both names appear in the same publication, *Lecythis ampla* is the more acceptable because its description is based on an unmutilated fruit.

The proper citation of the small-leaved, large-fruited *Lecythis* of Central America and Colombia is as follows:

Lecythis ampla Miers, Trans. Linn. Soc. London 30: 204, *pl. 43, figs. 1–2.* 1874.

L. ampullaria Miers, Trans. Linn. Soc. London 30: 201, *pl. 38, figs. 1–2.* 1874.
L. costaricensis Pittier, Contr. U. S. Natl. Herb. 12: 99–100, *pls. 6–8, figs. 3–4.* 1908.
L. armiliensis Pittier, Contr. U. S. Natl. Herb. 26: 9–10, *pl. 8.* 1927.

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Mori, S. 1971. The ecology and uses of the species of *Lecythis* in Central America. Turrialba 20: 344–350.
Pittier, H. 1908. The Lecythidaceae of Costa Rica. Contr. U. S. Natl. Herb. 12: 95–101.
———. 1927. The Lecythidaceae of Central America. Contr. U. S. Natl. Herb. 26: 1–14.

—*S. A. Mori, Summit Herbarium of the Missouri Botanical Garden, Drawer S, Balboa Heights, Canal Zone.*

CHROMOSOME NUMBERS OF PHANEROGAMS. 6.[1]

Chromosome numbers of phanerogams are reported below together with voucher data and herbaria where collections are deposited. Unless indicated otherwise the chromosome records are based on the study of one plant. Haploid counts are from pollen mother cells, and diploid counts are from root tips unless otherwise indicated.

Citations should have the form: Doe, J. 1974. *In* Chromosome numbers of phanerogams. 4. Ann. Missouri Bot. Gard. 61:

Count by **Tilton Davis, IV,** University of Missouri, St. Louis, Missouri 63121. Bud and seed material were received from Dr. J. L. Gentry at the Field Museum, Chicago.

Solanaceae

Jaltomata procumbens (Cav.) J. L. Gentry. $n = 12$. Costa Rica. prov. alajuela: near Poasito, 10°10′ N × 84°12′ W., *Gentry & Burger 2960* (F).

Counts by **Gerrit Davidse,** Missouri Botanical Garden and **Richard W. Pohl,** Iowa State University.

Gramineae

Brachyelytrum erectum (Schreb.) Beauv. $n = 11$. U.S.A. missouri: Washington Co., Clark National Forest, *Davidse 3492* (MO).

Echinochloa crusgalli (L.) Beauv. var. *crusgalli* $n = 27$. U.S.A. missouri: St. Charles Co., ca. 3 mi SW of Defiance, *Davidse 3524* (MO).

Elymus villosus Muhl. $n = 14$. U.S.A. missouri: Jefferson Co., ca. 5 mi E of Cedar Hill, *Davidse 3460* (MO).

Panicum lanuginosum Ell. $n = 9$. U.S.A. missouri: Jefferson Co., ca. 1 mi E of Cedar Hill, *Davidse 3449* (MO).

Panicum lindheimeri Nash. $n = 9$. U.S.A. missouri: Washington Co., Clark National Forest, *Davidse 3504* (MO).

Paspalum pubiflorum Rupr. ex Fourn. $n = 30$. U.S.A. missouri: Osage Co., Westphalia, *Pohl 12468* (ISC).

Zizaniopsis miliacea (Mich.) Doell & Aschers. $n = 12$. U.S.A. louisiana: La Fourche Parish, 4 mi W of Allemands, *Wooten s.n.* (ISC).

---

[1] The previous number in this series appeared in Ann. Missouri Bot. Gard. 61: 901–904.

The previous issue of the Annals of the Missouri Botanical Garden, Vol. 62, No. 1, pp. 1–224 was published on 9 April 1975.

Angiosperm Biogeography and Past Continental Movements

Peter H. Raven and Daniel I. Axelrod

"The isolation of land areas by sea-floor spreading, the uplift of new cordilleras, the emergence of new archipelagos and the disappearance of old ones, and the shifting positions of (some) landmasses have both created and destroyed environments to which biota have responded. In this sense, changing physical environments governed by plate tectonics have had a major role in evolutionary history. Plate tectonic theory thus provides a more reliable basis for analyzing changes in land-sea relations and changes in climates, and hence for interpreting problems of evolution and distribution, than has been available earlier. The reappraisal of the nature of the earth's crust by plate tectonic theory does not require any modifications of previously established major principles of evolution. However, it does demand that we recognize certain new principles of biogeography. . . .

"In the present paper, we examine the distributions of flowering plants, present and past, and attempt to interpret them in the light of newly available geological evidence. Although the field is vast, . . . we believe that an overview of angiosperm distributions in the light of geological history as now suggested by plate tectonic theory will be useful in suggesting new hypotheses and new directions for future research."

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ANNALS
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THE BASES OF ANGIOSPERM PHYLOGENY: INTRODUCTION

JAMES W. WALKER[1]

This issue of the *Annals of the Missouri Botanical Garden* contains papers presented at a symposium held during the 24th annual meeting of the AMERICAN INSTITUTE OF BIOLOGICAL SCIENCES, University of Massachusetts, Amherst, June, 1973, which was entitled "The Bases of Angiosperm Phylogeny." Joint sponsors of this symposium included the AMERICAN SOCIETY OF PLANT TAXONOMISTS, the Systematic, Paleobotanical, General, Phytochemical, and Developmental Sections of the BOTANICAL SOCIETY OF AMERICA, the SOCIETY FOR THE STUDY OF EVOLUTION, and the AMERICAN SOCIETY OF NATURALISTS. Arthur Cronquist graciously presided over the symposium. The symposium's theme was "a discussion of the characters and fields that are the bases of angiosperm phylogeny at the higher taxonomic levels, as they are related to the Takhtajan and Cronquist systems of angiosperm classification." Each participant was asked to answer two basic questions: (1) what are the principal characters in my particular field that are of phylogenetic significance at higher taxonomic levels in angiosperm systematics, and (2) how do these characters correlate with the Takhtajan (1969) and Cronquist (1968) systems of angiosperm classification.

The Takhtajan and Cronquist systems were chosen to provide a framework around which the review papers in this symposium could be organized because they are the most thoroughly documented of the recently published systems of angiosperm classification which have taken into consideration data from all bases of angiosperm phylogeny.

After some short remarks by Arthur Cronquist on angiosperm phylogeny and taxonomy in general, nine fields which have contributed to our knowledge of angiosperm systematics and phylogeny are reviewed. First, some phylogenetic contributions of floral morphology and floral anatomy are examined by Richard Eyde, and among other things centrifugal versus centripetal androecial development is shown not to be as valuable a phylogenetic indicator as previously thought.

[1] Department of Botany, University of Massachusetts, Amherst, Massachusetts 01002.

ANN. MISSOURI BOT. GARD. 62: 515–516. 1975.

Next, Leo Hickey and Jack Wolfe treat the field of vegetative morphology, emphasizing a little looked-at attribute of flowering plants, viz., leaf architecture. In the third paper in the symposium, William Dickison outlines the principal characters of vegetative anatomy which are of phylogenetic significance at the higher levels in angiosperm systematics, while pointing out that, currently, only evolutionary trends in secondary xylem and the phylogenetic conclusions that have resulted from recognizing these trends provide a firm basis for angiosperm phylogeny. Following this, Barbara Palser lists embryological characters which have proved to be phylogenetically useful at higher taxonomic levels (subclasses, orders, etc.), while indicating that, on the whole, embryological characteristics are remarkably constant at the family level. Next, through ultrastructure studies, H.-D. Behnke demonstrates taxonomic correlations based on the accumulation of storage products (starch versus protein) in sieve-element plastids. After this, contributions which palynology can make to angiosperm systematics and phylogeny are examined by James Walker and James Doyle, and it is shown, with some exceptions, that pollen morphology is consistent with the levels of relative advancement and the relationships postulated in the Takhtajan and Cronquist systems. This is followed by a broad cytotaxonomic review of chromosome numbers in flowering plants by Peter Raven, in which basic chromosome numbers are suggested for many higher taxonomic categories of angiosperms. Phylogenetic data from the field of chemotaxonomy are taken up next, including discussions covering the systematic contributions of plant natural products (by T. J. Mabry), serotaxonomy (by David Fairbrothers), amino acid sequencing (by Ronald Scogin), and nucleic acid hybridization (by T. J. Mabry), along with a general summary of the field by B. L. Turner. Next, phylogenetic contributions made by paleobotany are reviewed by Jack Wolfe (covering flower parts, fruits, seeds, and leaves), James Doyle (pollen), and Virginia Page (woods). The last paper in the symposium, by Ledyard Stebbins, is addressed to the question "Are deductions about transspecific evolution made through extrapolation from processes at the populational and species levels justified?" The papers prepared for this symposium clearly demonstrate the tremendous amount of systematic information available to contemporary taxonomists from the diverse fields of botanical inquiry that constitute the bases of angiosperm phylogeny.

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SOME THOUGHTS ON ANGIOSPERM PHYLOGENY AND TAXONOMY

ARTHUR CRONQUIST[1]

Since the time of Darwin, taxonomists have been concerned with phylogenetic relationships as well as with the formal taxonomic system. Some definitions of taxonomy have essentially equated it with phylogeny, as a study devoted to determining the evolutionary relationships among organisms. More recently, particularly in England, some botanists have tried to divorce taxonomy from phylogeny, reverting in this respect to pre-Darwinian days. Theirs is a natural reaction to the fact that the marriage of taxonomy to phylogeny has proved to be a rather difficult one.

It has become progressively clearer that a precise correlation of taxonomy with phylogeny is an unattainable goal. The more abundant the phylogenetic and other data, the more obvious the impossibility. Over and over again it turns out, when we have enough evidence, that before we can trace the members of a particular group back to a common ancestor, we are outside the confines of the group. The mammals, for which we have a very good fossil record, provide a case in point. No matter what set of criteria one chooses, there was never *an* original species of mammal, from which all other mammals are descended. The mammals originated as a set of more or less parallel evolutionary lines from reptiles—not just any old reptile, but from a particular group of reptiles during a particular span of geologic time. George Gaylord Simpson has for thirty years been using these facts to point out that the monophyletic criterion must be interpreted loosely if it is to be taxonomically useful. One way to put it is to say that if all the members of a particular taxon are descended from another taxon of lesser rank, the taxonomic criterion of monophylesis has been sufficiently met.

Once we admit the necessity for a loose interpretation of the monophyletic requirement, we are committed to the position that similarities due to evolutionary parallelism, as well as those due strictly to inheritance from a common ancestor, provide some indication of relationship and should be considered in the formulation of a taxonomic system. Insofar as the nature of the supply of mutations is a controlling force in evolution, the greater the genetic similarity between two groups, the greater the likelihood that they will produce similar mutations, have similar evolutionary potentialities, and undergo parallel evolutionary change. On phenotypic and genotypic bases, as well as on the basis of the nature of the supply of mutations, different groups have different evolutionary potentialities, and not all evolutionary channels are open to any one group. Insofar as natural selection is a controlling force in evolution, the greater the phenotypic and genotypic similarity between two groups, the greater their potentiality to undergo parallel evolutionary change. If the similarities resulting from parallelism are numerous and pervasive, then the ancestors were probably very similar to begin

[1] New York Botanical Garden, Bronx, New York 10458.

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with. Thus, a group defined on characters that turn out to reflect evolutionary parallelism may still meet, in some cases, the loose test of monophylesis that we have prescribed.

In spite of these difficulties with the application of the monophyletic criterion to taxonomy, it is clear (at least to me) that phylogenetic considerations have a proper role to play in the establishment of taxonomic systems. The true function of taxonomy is to produce a system of classification of organisms that best reflects the totality of their similarities and differences. Since we have significant data on only a small fraction of the total number of characters of organisms (especially characters that do not have an obvious morphologic expression), the system needs to be set up in such a way that new data, as they are acquired, will tend to fit in harmoniously, rather than being at cross purposes to it. This will be true only if the system is in broad-scale harmony with evolutionary relationships.

It is possible to perceive natural groups without thinking in terms of evolution, as indeed taxonomists did B.D. (Before Darwin), but such perception is facilitated by an evolutionary frame of reference. The transfer of the Salicaceae and Cucurbitaceae from the subclasses Hamamelidae and Asteridae, respectively, to the subclass Dilleniidae reflects evolutionary thinking rather than simple phenotypic comparison in a theoretical vacuum.

The taxonomic system needs to be so constructed that a logically possible and reasonably monophyletic evolutionary scheme can be devised for it. The more information we have, the fewer will be the possible alternatives in such a procedure. On the information available to him, Engler could include the Salicaceae with his other Amentiferae, and treat the Amentiferae as the most primitive group of dicotyledons. On the information available to us now, modern taxonomists can do neither. Bentham and Hooker could insert the gymnosperms between the monocotyledons and dicotyledons, and treat all three groups at the same rank. No one would propose to do so now.

The development of a taxonomic scheme and a phylogenetic interpretation properly proceed in close association, each influencing the other.

The fossil record has only recently begun to be very useful in major taxonomic and phylogenetic interpretations in the angiosperms. The scanning electron microscope has greatly increased the utility of pollen in this regard, and the palynological data have been one of the factors leading to a reconsideration of the megafossils. A comprehensive reinterpretation of the Potomac early Cretaceous angiosperm fossils is underway but not yet published. I do not want to publicly anticipate the results of Drs. Doyle, Hickey, and Wolfe, but I will say that insofar as I am acquainted with these results, they are compatible with my previous views. Doyle has already published enough about fossil pollen to give strong support to the view, originally put forward primarily on the basis of comparison of modern taxa, that the monosulcate pollen type is primitive among the angiosperms.

For the present, at least, comparative structure of modern forms, from the eyeball to the SEM level, remains the mainstay of major taxonomic interpretation. Chemical and serological data of various sorts are beginning to find their use also. The time and effort required to obtain information of these sorts, how-

ever, insures that morphology, in the broad sense, will continue to reign taxonomically supreme for some years to come.

We should recognize, of course, that morphological characters have a chemical foundation. All characters are eventually chemical, and what we commonly call chemical characters are really just the ones without a known morphological expression. Chemical characters, as so defined, are intrinsically neither more nor less significant taxonomically than morphological ones. It all depends on how well they correlate with other characters.

One of the fundamental taxonomic principles that most of us are comfortable with is that taxonomy proceeds by the recognition of multiple correlations. A corollary of this principle is that individual characters are only as important as they prove to be in marking groups that have been recognized on a larger set of information. It is a natural assumption that once the value of a character in a particular group has been established in this way, it can be applied fairly uniformly across the board in other groups. This assumption is false, and has to be unlearned by each successive generation of taxonomists. There is just enough tendency for consistency in the value of taxonomic characters to mislead the unwary. One of my colleagues in another country has summarized the situation by paraphrasing Orwell: All characters are equal, but some are more equal than others.

We often hear the idea nowadays, that when we can get down to the level of the chemical structure of the gene we will have a better set of characters, which will enable us to find out the *real* relationships among organisms. Then we can downgrade or dispense with the traditional phenotypic characters, which lose validity because they are so many steps removed from the genes that govern them. This idea is a beguiling fallacy. Genes are important, not for their own sake, but for what they do. They are important because of their influence on the phenotype. The fundamental concern of human beings in considering organisms is the nature of the phenotype. In order to understand the phenotypes, we begin by trying to distinguish genetic from environmental influences. In pursuit of understanding genetic influences we are led eventually to the gene. Certainly an understanding of the detailed chemical composition and structure of genes is potentially helpful to the taxonomist, and I welcome efforts in this direction. At the same time, we cannot expect to have a high batting average in predicting phenotypic effects from genic composition. A chemical difference that seems small to us might have a disproportionately large phenotypic effect, and vice versa. We can no more predict the phenotype directly from the genes than we could predict the double helix from a study of nuclear physics.

Finally, a bit of philosophizing about how to recognize phylogenetic relationships. We must first recognize that Bessey was right in emphasizing that plant relationships are up and down phylogenetic lines, rather than crosswise. A useful way of perceiving relationships, then, is to find out what is going on in a group, and then mentally extrapolate backwards from the more primitive known members. Oftentimes some other group will then emerge as likely ancestors. Similarities between advanced members of two groups, on the other hand, are significant only insofar as they indicate similar evolutionary potentialities in the

primitive members. As we have pointed out, such similarities are not to be ignored, but they are only part of the evidence, to be weighed along with all the rest of the evidence. The angiosperms as a whole are so beset with parallelism that the taxonomic and phylogenetic significance of individual similarities is often minimal.

One must also put in the caveat that when one taxon is said to be ancestral to another, it does not necessarily mean that any existing member of the first group is the surviving ancestor of the second. It merely means that if we had the ancestor, we would put it in that group. No existing reptile is ancestral to the mammals, but the mammals originated from reptiles all the same.

Let us take the Asteraceae as an example for the extrapolation principle. The fossil record of the Asteraceae is still too scanty to be very useful. On the basis of comparison of modern members of the family, it is clear that aggregation and reduction of the inflorescence have been pervasive features in the evolution of the family. Furthermore, it appears that the primitive composites must have been woody plants with opposite leaves and a basically cymose inflorescence structure. If we then extrapolate backwards from these opposite-leaved, woody plants to something with a less condensed, basically cymose inflorescence, where do we land? Certainly not in the alternate-leaved, essentially herbaceous order Campanulales, which has often been taken as ancestral to the Asteraceae. Instead, the Rubiales and the more primitive members of the Dipsacales are suggested. Even the specialized pollen presentation mechanism, which has been used to link the Asterales to the Campanulales, occurs also in some members of the Rubiaceae. The features here discussed do not prove that the Asterales are derived from the Rubiales or Dipsacales, but they do provide a lead to be investigated. That investigation leads me to believe that the ancestry of the Asterales lies in or near the Rubiales.

THE BASES OF ANGIOSPERM PHYLOGENY: FLORAL ANATOMY

Richard H. Eyde[1]

Abstract

An eclectic ramble through phylogenetic aspects of floral structure includes the following: (1) Sterling's view that the ancestral flowers of Rosaceae had only two ovules per carpel is examined and rejected. (2) Recent observations on the direction of androecial development in various taxa are reviewed, and it is concluded that centrifugality is not as valuable a phylogenetic indicator as some systematists had hoped it would be. (3) An attempt is made to reinterpret the inverted placental bundles of Capparales and the inverted "recurrent" bundles of *Nestronia* along morphogenetic lines. It is suggested that the inverted orientation is causally related to the initiation and differentiation of these bundles in isolation from previously formed vascular tissue.

Floral anatomy turns some botanists into fantasts, others into iconoclasts. But despite the frequent speculative excesses, the occasional overreaction, and the recurring disagreements that are a part of the field, serially sectioned and cleared flowers continue to provide essential phylogenetic information. To begin with a straightforward example, consider Cronquist's (1968) suggestion concerning the origin of the Proteales, which he defines as Proteaceae plus Elaeagnaceae. Stressing similarities between the Proteales and the Thymelaeaceae (a point of difference with Takhtajan, 1970[2]), Cronquist postulates that the origin of the order was in the Myrtales. For this to be true, the gynoecium in Proteaceae and Elaeagnaceae must be pseudomonomerous; in other words, it must be a syncarpous gynoecium that has acquired through evolutionary processes the superficial appearance of a single carpel. Noting that the Myrtales, which are syncarpous, must be excluded as possible ancestors if the gynoecium of the Proteales should turn out to be a solitary carpel, Cronquist adds: "The most likely origin of the Proteales would then be in the Rosales." Serial cross sections through the gynoecia of various Proteaceae make Cronquist's favored position for the Proteales untenable, for there is no sign of pseudomonomery. Instead, each gynoecium has the three major vascular bundles and the ventral suture of a single carpel (Fig. 1). The same is true of Elaeagnaceae (Fig. 2; see also Eckardt, 1937: 47). The ancestry of the Proteales must therefore be sought in a group with apocarpous members such as Cronquist's Rosales or Takhtajan's Saxifragales.

The conviction that an apocarpous gynoecium did not originate from a syncarpous gynoecium will not be challenged in this forum because evidence is overwhelming that apocarpy preceded syncarpy in many groups of flowering

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[1] Department of Botany, Smithsonian Institution, Washington, D.C. 20560.

[2] I cite the Russian version of Takhtajan's *Flowering Plants: Origin and Dispersal* (1970) rather than the English version (1969). Although the English version was translated from a Russian manuscript, the printed Russian version appeared later and differs in a number of ways (see, for instance, the newly segregated families in Cornales). While my symposium contribution awaited publication, Fischer Verlag published a German version: *Evolution und Ausbreitung der Blütenpflanzen* (1973).

Ann. Missouri Bot. Gard. 62: 521–537. 1975.

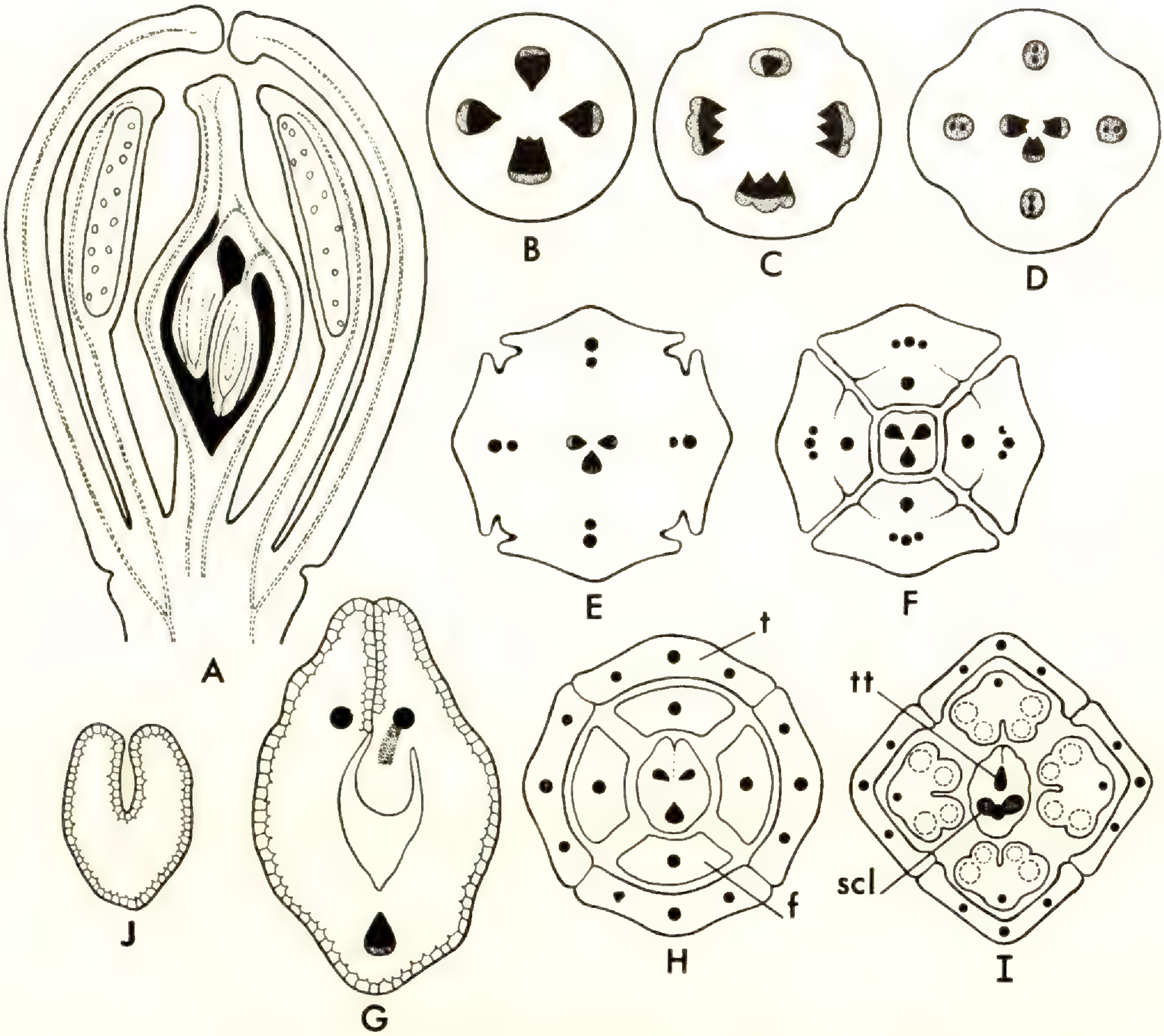

FIGURE 1. Floral anatomy of *Bellendena montana*; redrawn from Venkata Rao (1971).—A. Longitudinal section.—B–I. Cross sections at various levels from base to apex.—J. Young carpel in cross section. f = filament; scl = sclerenchyma; t = tepal; tt = pollen-transmitting tissue. Venkata Rao's monograph contains similar illustrations for a number of other Proteaceae; in every case the gynoecium is shown to be a single carpel. This figure and those that follow redrawn by A. Tangerini.

plants. I know of no group in which the reverse change is believed to have occurred, and it is difficult to imagine a modification of ontogenetic events that would produce such a reversal. Similarly, I know of no group in which markedly zygomorphic flowers are considered antecedent to actinomorphic flowers, nor do I know of a group in which a pluriovulate gynoecium is thought to have evolved from a 1-ovulate gynoecium. A number of other widespread evolutionary trends in floral structure are now known to reverse at least occasionally. In the araliaceous genus *Tetraplasandra*, a completely superior ovary has evolved secondarily from ancestors with completely inferior ovaries (Eyde & Tseng, 1969).[3] In the Onagraceae, the apparently primitive fuchsias have perianth

[3] The argument for secondary hypogyny in *Tetraplasandra* involved derivation of the Hawaiian species from tetraplasandras of the western Pacific. Philipson (1970) subsequently redefined the genus *Gastonia* so as to include the extra-Hawaiian tetraplasandras (see also

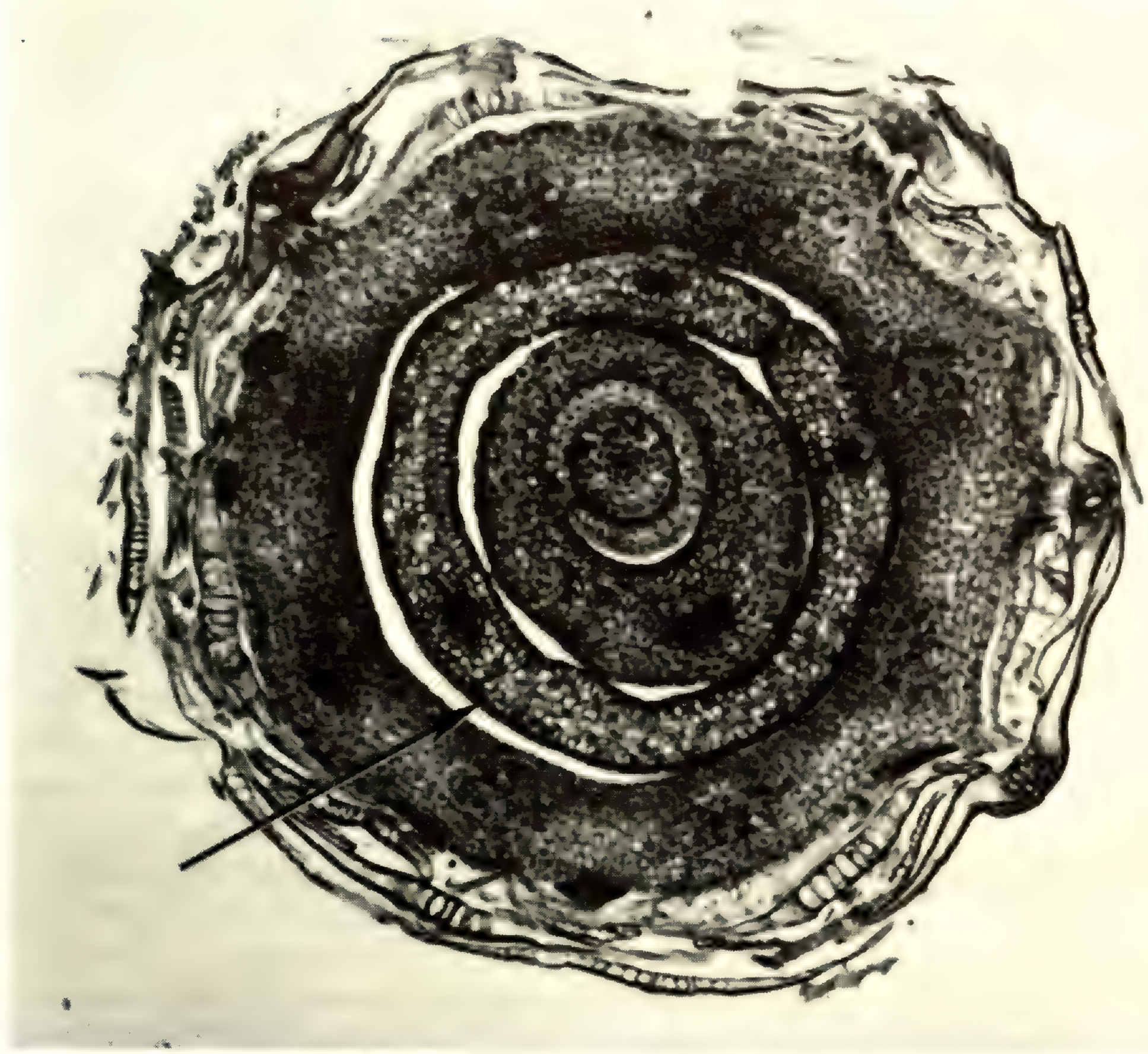

FIGURE 2. Cross section through flower of *Elaeagnus umbellata* (cultivated, Plant Introduction Station, Glendale, Maryland); × 100. Note single carpel (arrow) surrounded by floral tube. Photo by V. Krantz.

members united basally in a floral tube, the general condition in Myrtales. Evolution of the more specialized onagraceous genus *Lopezia* involved the loss of the floral tube: floral parts are separate in lopezias that are nearest the ancestry of the genus (Eyde & Morgan, 1973; Plitmann, et al., 1973). However, a floral tube has evolved secondarily in two specialized species of *Lopezia*; so the shift from sympetaly to choripetaly and back to sympetaly may not be as genetically and developmentally difficult as has been suggested (Stebbins, 1967: 138).

Although the general evolutionary trend in angiosperms has been from many floral parts to few, several cases of secondary increase in the number of perianth parts are known (Stebbins, 1967), and a good experimental beginning has been made toward understanding the hereditary and selective basis for such an increase (Huether, 1968, 1969; Stebbins, 1968, 1970). Convincing examples of

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Stone, 1972). This change does not weaken the case for secondary hypogyny because the close relationship of *Tetraplasandra* to *Gastonia* is not in doubt. To accord with Philipson's taxonomy, the epigynous flower shown diagrammatically in our article (Eyde & Tseng, 1969, fig. 1) should be labeled *Gastonia papuana*.

evolutionary increase in stamen number, presumably associated with shifts in pollination ecology, are so numerous that an investigator who wishes to develop a satisfactory evolutionary scheme for a group with a high number of stamens at one extreme and few stamens at the other is now well advised to start by hypothesizing an intermediate number of stamens as the ancestral condition.

Of course, the initial idea or argument must be tested by considering all available information that might tend to contradict it. If associated characters, known evolutionary processes and developmental mechanisms, geographic and environmental distribution, or the fossil record do not accord with the initial hypothesis, the discrepancies must be explained or the hypothesis changed. Another test for evolutionary sequences can be expressed as a question: Does the sequence lead back to an ancestral state that can also be ancestral for groups closely related to the group under consideration?

If adjoining groups are known and if the postulated evolutionary trend fails to lead back to a common ancestry with the adjoining groups, something is wrong. Thus, I have been led to reexamine Sterling's (1966b, 1969) contention that the ancestral Rosaceae probably had only two ovules per carpel. With rare exceptions (see Kania, 1973), systematists agree that the Rosaceae had a close common origin with Cunoniaceae, Davidsoniaceae, Hydrangeaceae, etc. (Takhtajan's Saxifragales). The entire alliance, subclass Rosidae, is believed to have arisen from the Magnoliidae either directly (Cronquist) or by divergence from the line leading to the Dilleniales (Takhtajan). An economical interpretation of this lineage, as it concerns ovules, is that the multiovulate condition primitive for angiosperms was retained in the early Rosales (Cronquist, 1968: 229) and still prevails in certain Rosaceae. The Spiraeoideae are generally considered the primitive subfamily of Rosaceae: carpels are mostly separate, free from the floral tube, follicular at maturity, and they are multiovulate in about half the species. Scalariform perforation plates, rare in Rosaceae, have been found in the woods of two multiovulate spiraeoid genera, *Quillaja* and *Neillia* (fide Takhtajan, 1966). Subfamily Maloideae (Pomoideae), characterized by an inferior gynoecium, is generally considered a derivative group. The basic maloid chromosome number, $x = 17$, is surely derived, and the suggestion of Stebbins (1950, 1958)—based upon earlier cytological work of Sax—concerning the allopolyploid origin of this group from prunoid ($x = 8$) and spiraeoid ($x = 9$) parentage has been well received.

The existence of a spiraeoid with the maloid chromosome number—*Quillaja brasiliensis*, $2n = 34$ (Bowden, 1945)—is problematical and could be due to allopolyploidy within the Spiraeoideae from primitive forms having $x = 8$ (i.e., an *Exochorda* ancestor) and $x = 9$. However, a recent chemotaxonomic survey has shown that whereas flavone C-glycosides are present in eight genera of the Maloideae, they are restricted in the Spiraeoideae to *Quillaja*. Therefore, *Quillaja* could be a relict of early precursors of the Maloideae that were far more spiraeoid-like than the modern maloids (Challice, in press).[4]

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[4] J. S. Challice (Long Ashton Research Station, University of Bristol) kindly read a preliminary version of this contribution and suggested changes, which I have incorporated. It should be noted that the ancestry of Maloideae as reconstructed by Stebbins differs from

Sterling rejects a spiraeoid parentage for the Maloideae. He suggests instead that both groups have evolved independently from a remote common ancestor, a suggestion based on the way in which the 2-ovulate condition is associated with other characters of the gynoecium. Fundamental to Sterling's reasoning is the assumption that the ventral sutures of carpels close progressively in the course of evolution. Carpels that are unsealed at the level of ovular insertion (insertion of lowermost ovules in multiovulate carpels) are assumed to be more primitive than carpels that are closed at this level. Sterling (1966b) first suggested that the 2-ovulate condition is primitive for both Spiraeoideae and Maloideae, but subsequent chi-square analysis caused him to abandon this view for Spiraeoideae (Sterling, 1969). By his own criterion, the spiraeoids are primitively multiovulate.

Sterling's persistence in the view that two ovules are primitive for Maloideae and for the family rests on a chi-square probability calculation for 15 species of maloids with more than two ovules per carpel. Twelve of the 15 species have closed sutures. The objection might be raised that the open carpel is not a reliable indicator of primitiveness (Carlquist, 1969: 354); however, the way in which Sterling has shown other gynoecial characters to be associated with this feature seems to justify the assumption that open sutures are, in general, more primitive than closed sutures in the Rosaceae. The problem in applying this generalization to the maloids is that 11 of the multiovulate species in Sterling's calculation belong to three closely related genera: *Chaenomeles*, *Cydonia*, and *Docynia* (Sterling, 1966a). To explain the association of the (basally) closed suture with the multiovulate condition, one need only postulate a slight reversal of the general evolutionary trend for sutural closing early in the ancestry of this one group of three genera. If the three genera are removed from consideration, the remaining maloid species with more than two ovules per locule do not support Sterling's conclusion. To be sure, *Sorbus americana*, which can have a third ovule in some of its locules, has closed sutures; but *Eriobotrya philippinensis*, in which Sterling saw one example of an extra ovule, has open sutures; *Raphiolepis indica*, which commonly has three or four ovules per locule, has open sutures; and *Malus astracanica*, with two superposed pairs of ovules per locule, also has open sutures (Sterling, 1965a, 1965b).

The organizer of our symposium asked each contributor to discuss characters that distinguish major taxonomic groups. I can think of no floral characters found in all members of one and only one class or subclass. Five-merous flowers are found only among the dicotyledons, but many dicotyledons have flowers that are not 5-merous. Similarly, septal nectaries are found only among the monocotyledons, but because of their limited distribution, septal nectaries can hardly be called a distinguishing feature of monocotyledons. From pre-Linnaean and early post-Linnaean times, specialized structural configurations of the in-

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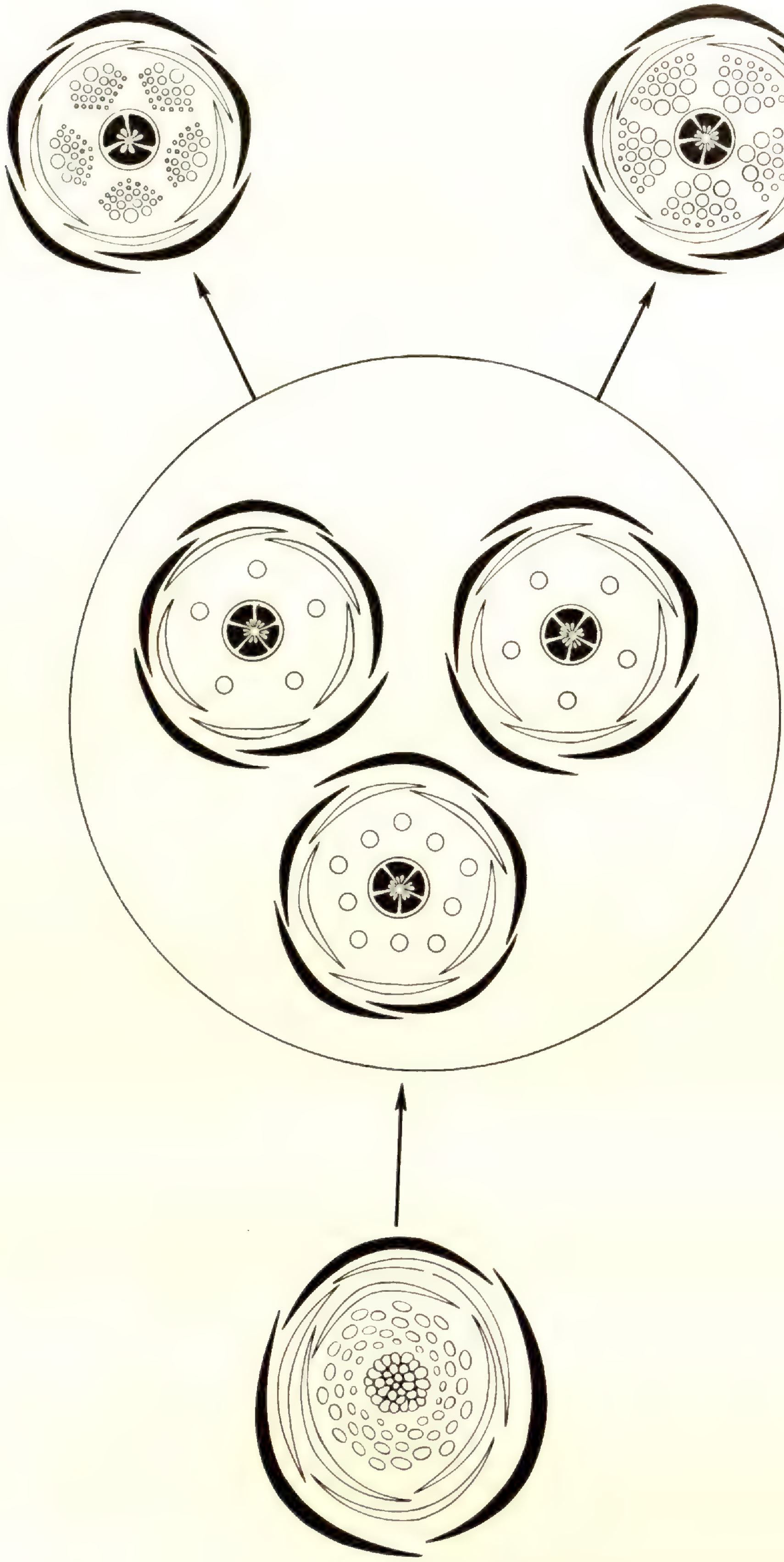
the ancestry (spiraeoid only) suggested by Gladkova (1972). Moreover, the position of *Exochorda*, which Stebbins (1958) considered a possible living link between Prunoideae and Maloideae, is uncertain. Chemotaxonomic investigations indicate closer links between *Prunus* (Prunoideae), *Sorbaria* (Spiraeoideae), and the maloid genera *Pyrus* and *Malus* (Challice, 1972, 1973). [The part of my manuscript dealing with Rosaceae was last revised in June 1974.]



florescence, flower, and fruit have been important for the recognition of certain groups we now call families; e.g., Umbelliferae, Compositae, Cruciferae. In general, however, a number of more or less widespread traits must be used in combination to characterize families and categories higher than families. Examples are easily found by scanning Cronquist's (1968) synoptical arrangements. As Stebbins (1967, 1970, this symposium) has reiterated, floral characters that aid in delimiting a family or an order in one part of the system are of value only at the specific or the generic level elsewhere in the system.

Some workers have treated the order in which stamens develop as a fundamental systematic feature. Noting that certain dicotyledonous families with polymerous androecia produce the stamen primordia in a centrifugal direction—first-formed primordia nearest the center of the flowers, last-formed primordia nearest the perianth lobes—Corner (1946) proposed that the centrifugal mode of development defines "a natural phylum" derived from ancestors with centripetal androecia. Cronquist's preliminary outline for dicotyledons incorporated Corner's proposal: the two main evolutionary lines derived from the primitive angiosperms are distinguished by the direction of androecial development (Cronquist, 1957). Eames (1961: 107) also took note of centrifugal androecia but attributed less importance to the phenomenon because he thought that the centrifugal sequence occurs in the primitive Winteraceae (Eames, 1961: 386) as well as in more derivative groups. Others have pointed out, however, that stamen primordia of Winteraceae arise centripetally (Sampson, 1963; Tucker, 1972).

Leins (1964) speculated that the centrifugal androecium did not evolve directly from primitive angiosperms with numerous spirally arranged parts but through an intermediate cyclic stage with few stamens arranged in one or two whorls (Fig. 3). From the cyclic stage, Leins derived a *Rosiflorenast* with concave floral meristems and a *Guttiferenast* with convex floral meristems. Basipetal "dedoublement" (secondary evolutionary increase in the number of primordia) in both lines—dedoublement on the ventral side in the *Rosiflorenast*, dedoublement on the dorsal side in the *Guttiferenast*—would account for the difference between centripetal and centrifugal androecia. Hiepko (1965) endorsed the idea of secondary polyandry through dedoublement but pointed out that the centrifugal androecium is not always associated with a concave meristem. Leins (1971) subsequently offered an alternative scheme involving three separate evolutionary lines for dicotyledons with polymerous androecia (Fig. 4). The members of one line have primitively simple stamens; that is, each stamen is considered a unit floral appendage. The corresponding units in the two remaining lines are thought to be complex structures, dorsally divided in one line, ventrally divided in the other. In this alternative scheme, there is no intermediate

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FIGURE 3. Leins's (1971) diagrammatic representation of a theory that he proposed in 1964. According to this theory, ancestral dicotyledons had numerous simple, spirally arranged, centripetally developed stamens. Androecia with one or two whorls of simple stamens (within the circle) are derived directly from the ancestral condition. Certain centripetal androecia (upper left) and all centrifugal androecia (upper right) are derived from the cyclic stage by fragmentation of the whorled stamen primordia.

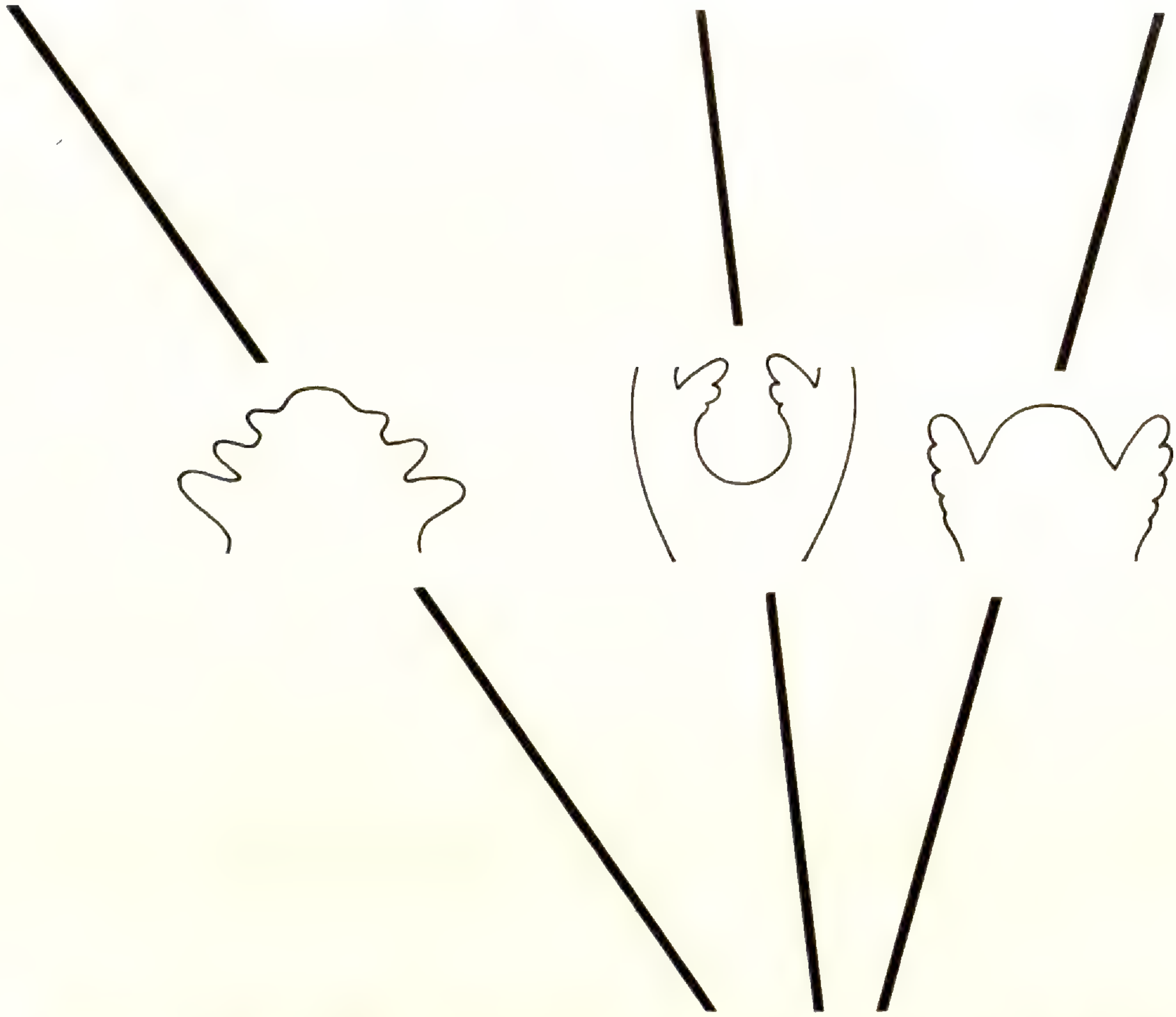
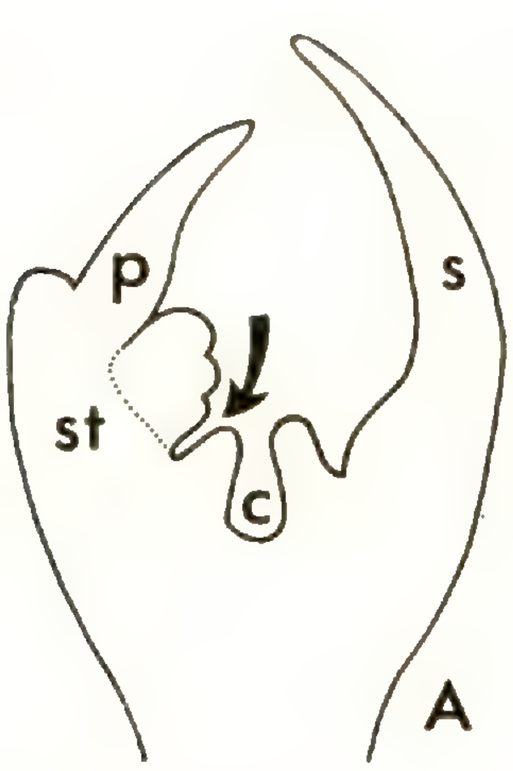
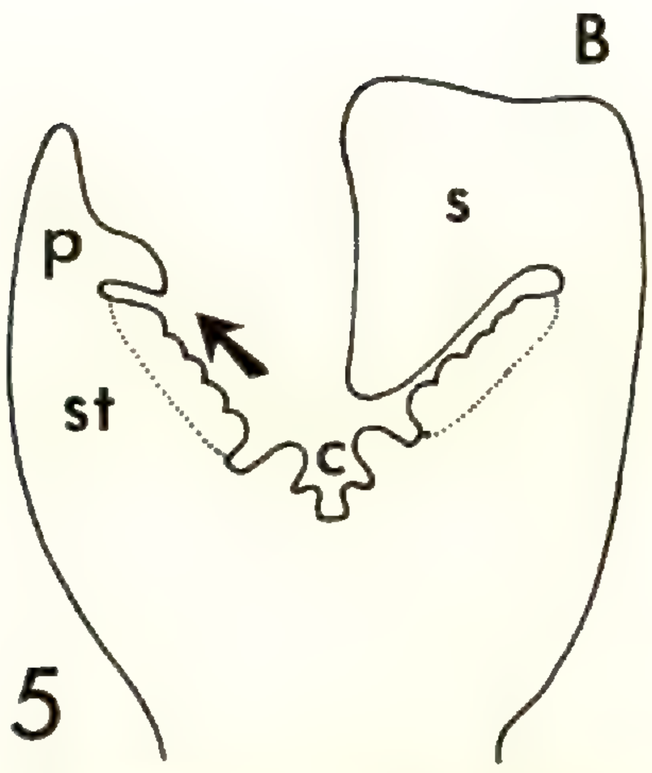


FIGURE 4. Leins's (1971) alternative evolutionary scheme for dicotyledons. Here Leins envisions early divergence of three evolutionary lines, all with polymerous androecia. In the line on the left, stamens are initiated centripetally in a spiral. The other two lines correspond to the two derived groups in Fig. 3. Oligomerous androecia of one or two whorls can evolve from all three lines.

cyclic stage. The three types of androecium are visualized as having evolved independently from remote precursors, and the Magnoliidae are not considered ancestral to all other dicotyledons (see also Kubitzki, 1969, 1972).

Although Cronquist (1968: 92, 191) rejects the notion that centrifugality must be associated with a secondary increase in stamen number, the centrifugal androecium remains an important element in the construction of his system. It is the principal character for separating subclasses Rosidae and Dilleniidae (pp. 130–132) and for separating the Dilleniales from the Magnoliidae (pp. 187, 191). Moreover, the centrifugal androecium figures prominently in his decision to place the Paeoniaceae and the Crossosomataceae in the Dilleniales (p. 192). Centrifugality is also one of the factors mentioned to explain the wide separation of the Papaveraceae from the Capparaceae (pp. 155, 214) and the Lecythidaceae from the Myrtales (p. 202). It is of interest that Merxmüller & Leins (1971) report centripetal development of the androecium in *Begonia*. For those who consider centrifugality a fundamental trait, this raises doubts concerning Cron-





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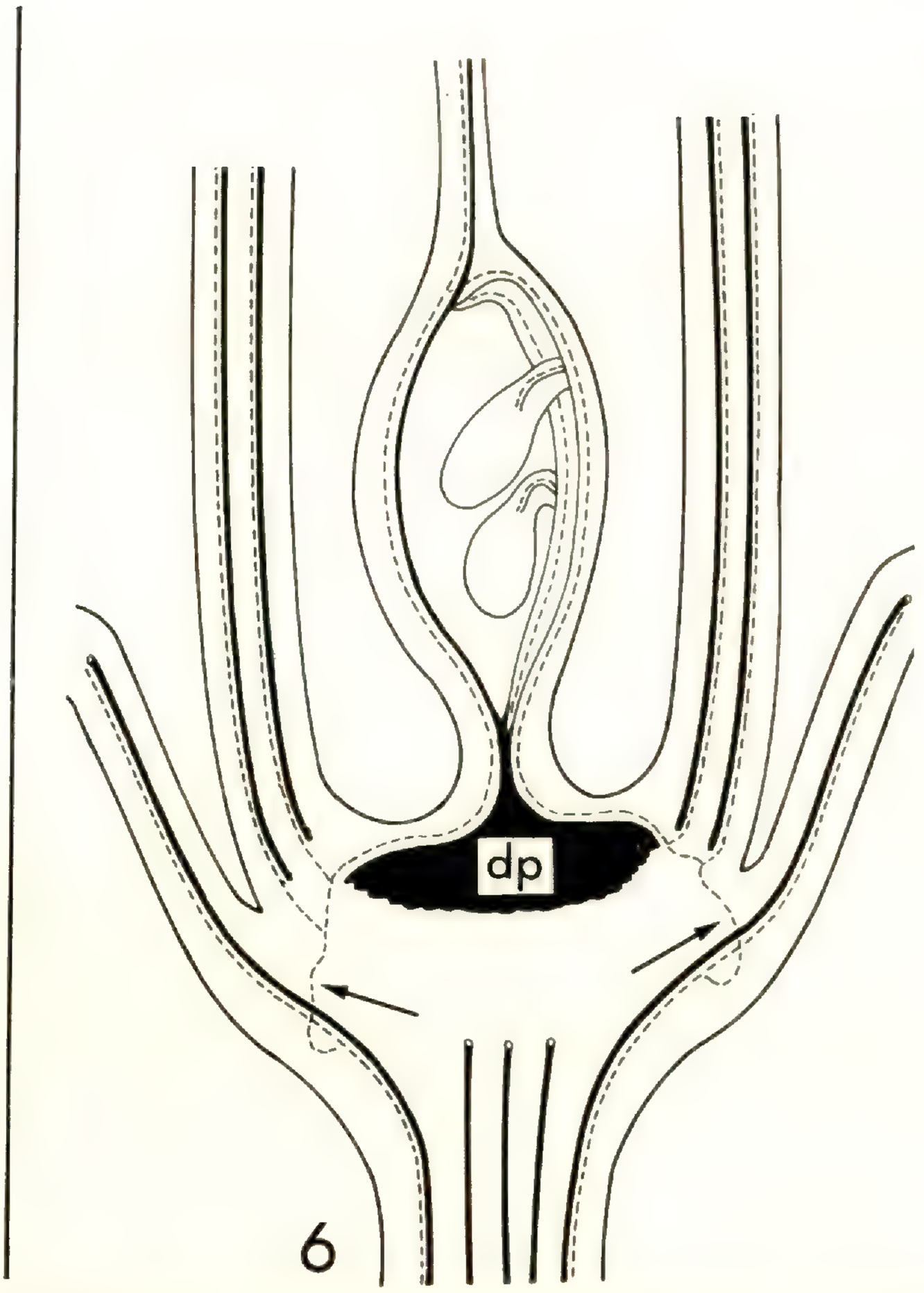

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FIGURES 5–6.—5. Centripetal (A) and centrifugal (B) androecial development in Myrtales; redrawn from Mayr (1969).—A. *Melaleuca* (Myrtaceae).—B. *Punica* (Punicaceae). c, p, s, st, indicate primordia of carpels, petals, sepals, and stamens, respectively.—6. Diagrammatic longitudinal section through basal portion of a flower of *Petalostemon* (Psoraleae, Leguminosae); redrawn from Lersten & Wemple (1966). Heavy lines represent xylem; broken lines, phloem. The discontinuity plate (dp) is a unique feature of this tribe. Vascular continuity is maintained by phloem alone (arrows).

quist's assignment of the Begoniaceae to the Violales. Violales, when multistaminate, have a centrifugal androecium.

Takhtajan's placement of most of these taxa is fairly similar to Cronquist's; however, Takhtajan's lesser emphasis on the centrifugal androecium is evident in his treatment of the Lecythidaceae. Although he summarizes Cronquist's argument concerning the family, he retains the Lecythidaceae in the Myrtales (Takhtajan, 1970: 119; see also Takhtajan, 1959: 226).

As Cronquist (1968: 91) was aware, the stamens in certain members of the Alismatales develop centrifugally, whereas development is centripetal in other members (Kaul, 1967, 1968; Leins & Stadler, 1973). Kaul believes the centrifugal condition is primitive for the group in which it occurs. If Kaul is right, the phylogeny of the Alismatales involves an evolutionary reversal from centrifugal development to the centripetal development characteristic of the most primitive

angiosperms. To be sure, an evolutionary reversal within the monocotyledons need not guide our thinking concerning dicotyledons; however, recent observations on dicotyledons also suggest that the direction of androecial development is reversible. *Glaucidium* has been found to have a centrifugal androecium (Tamura, 1972). In Cronquist's system *Glaucidium* is a member of the Ranunculaceae, in which all other members have centripetal androecia. Takhtajan considers *Glaucidium* the only genus of a separate family Glaucidiaceae, said to link Ranunculaceae with Papaveraceae, another family with centripetal stamens. Sawada (1971) reports that *Paeonia japonica* has centripetal stamens, unlike other peonies, which produce their stamens centrifugally (Kubitzki, 1972, challenges Sawada's observation). Investigating the Myrtales, Mayr (1969) observed that *Lagerstroemia* (Lythraceae) and *Punica* (Punicaceae) have centrifugal stamens in contrast to the centripetal stamens of Myrtaceae (Fig. 5). The Onagraceae, though not polyandrous, are developmentally more similar to *Lagerstroemia* and *Punica* than to the Myrtaceae. If the direction of androecial development is a character of fundamental importance, Mayr pointed out, her observations make the Myrtales an unnatural group despite the many characters that they have in common. The Lythraceae, Onagraceae, and Punicaceae would have to be moved to Leins's *Guttiferenast*—subclass Dilleniidae of Cronquist and Takhtajan—while the Myrtaceae remain in the Rosidae. Although the differences between centrifugal androecia and centripetal androecia are striking (Tucker, 1972), it now appears that centrifugality is not nearly as valuable a phylogenetic indicator as some systematists had hoped it would be (see also Sattler, 1972).[5]

No aspect of floral structure has been more intensively studied or more controversial than vascular anatomy. Attempts to interpret all flowers according to a single vascular "plan" have not been completely successful, and one reason for this may be that the earliest angiosperms were a diverse lot with respect to floral vasculature. Ancestral diversity is suggested by the varied vascular patterns of living Magnoliidae. Ovules can be vascularized by branches from the dorsal carpel bundles in addition to, or instead of, branches from the ventral bundles. Several taxa have double dorsal bundles (Tucker & Gifford, 1964: 201) or "extra" bundles of other kinds (see Payne & Seago, 1968: 580). An outer series of bundles (cortical system) accompanies an inner "stelar" system in flowers of various members of the Annonaceae, Calycanthaceae, Magnoliaceae, and Myristicaceae (Sastri, 1969). The discovery of a cortical system in flowers of *Paeonia japonica* suggests that the Paeoniaceae should be moved to the Magnoliidae from the Dilleniidae, where Cronquist and Takhtajan put the family, especially if the direction of androecial development is no longer an impediment to the transfer (Sawada, 1971).

Vascular peculiarities of the flower have phylogenetic significance in a number of other groups. The discontinuity plate (Fig. 6), a unique horizontal proliferation of tracheary elements beneath the ovaries in the tribe Psoraleae of the Leguminosae (Lersten & Wemple, 1966) aids in defining the tribe, and it

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[5] Sattler's article, which I saw after this symposium, points out that the androecium of *Ochna* (Dilleniidae) has been found to develop centripetally. The work by Leins & Winhard (1973) on Loasaceae is also relevant, as is Stebbins's (1974: 220ff) most recent book.

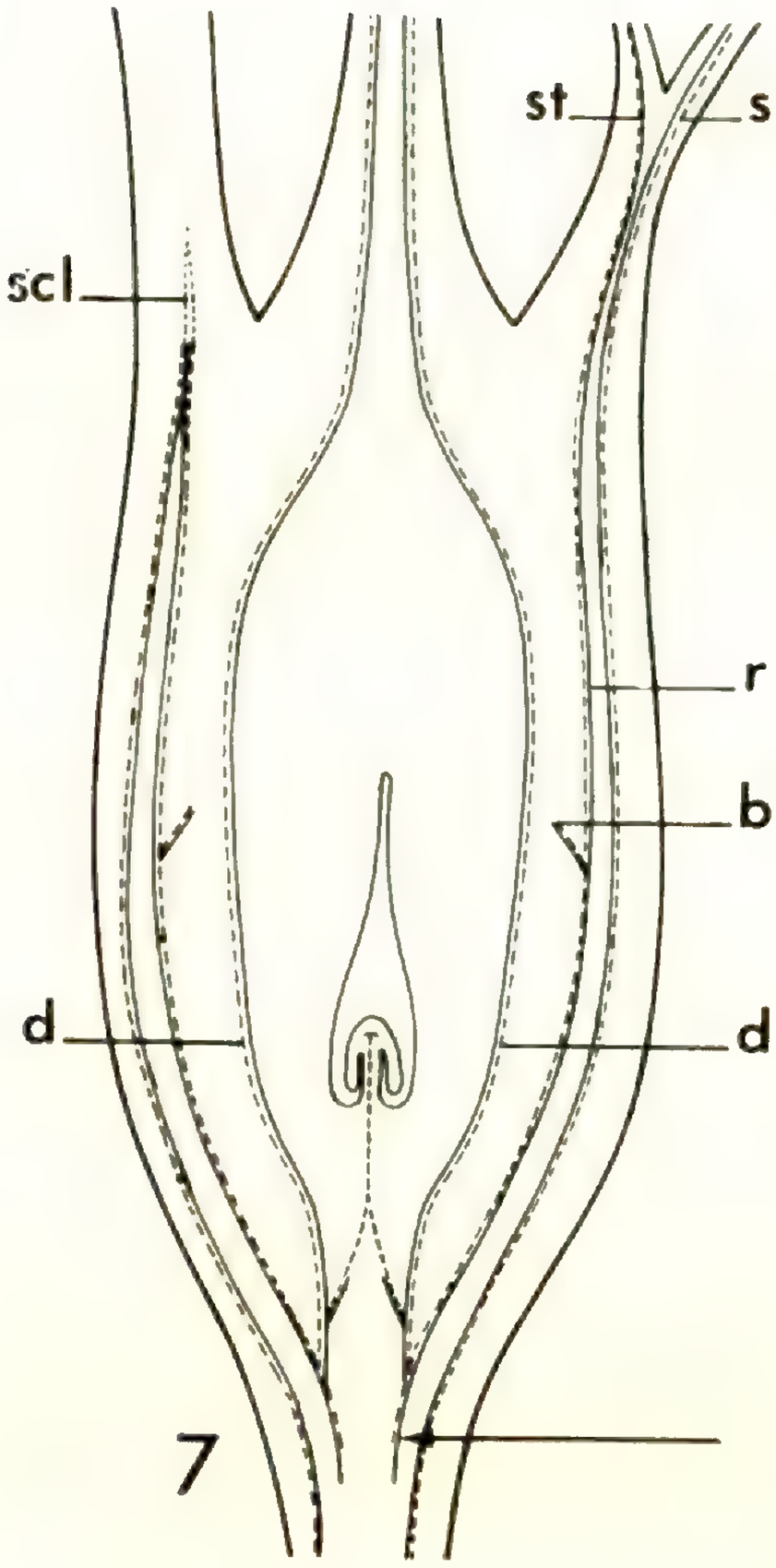
identifies *Psoralea* as the primitive genus, for within *Psoralea* one finds transitions between the discontinuity plate and normal floral vasculature. As a rule, ovules borne on axile placentas receive branches from bundles running vertically through the center of the ovary. In some taxa, however, the ovules are supplied by transeptal bundles, i.e., bundles running transversely through the septa. Both kinds of ovular supply occur in the Myrtaceae: Schmid (1972b) stresses this feature in separating *Eugenia*, with transeptal bundles, from *Syzygium*, with axile bundles.

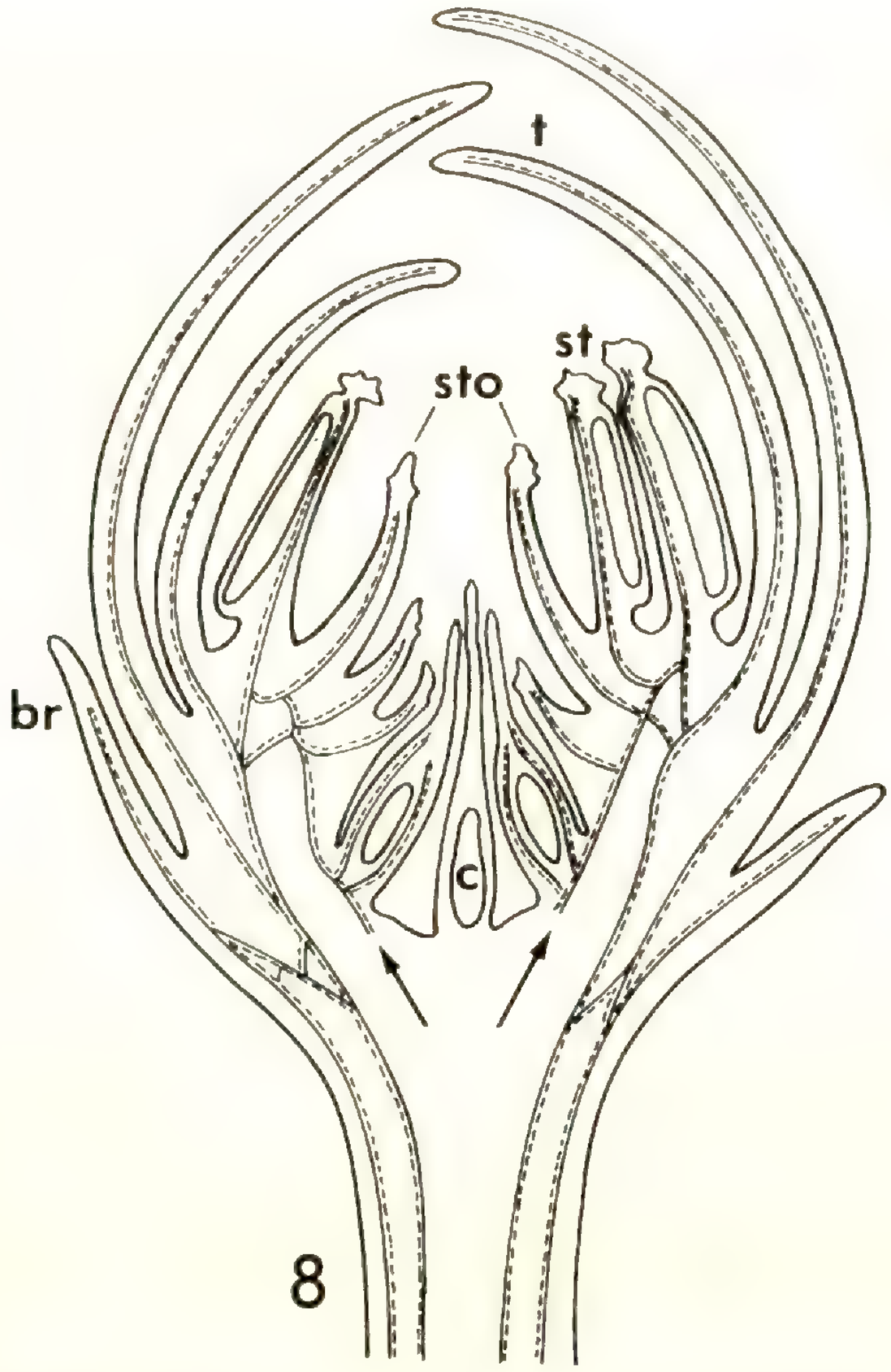
No doubt the axile pattern is ancestral to the transeptal pattern. Phylogenetic applications are presently limited, however, because clear-cut transitions from the axile to the transeptal condition are hard to find. Schmid has found transeptal bundles to be prevalent in the myrtoid subfamily of the Myrtaceae, and I have found transeptal bundles to be universal in the Onagraceae. We are hopeful that further study of this interesting feature will clarify family affinities within the Myrtales.

The ancestral vascular system of rosaceous carpels probably consisted of five major bundles: a dorsal bundle, two ovular bundles running through the carpel margins to the ovules, and two wing bundles running more or less parallel to the ovular bundles but extending into the style. Various modifications of this basic structure are illustrated in Sterling's 10-paper series (see Sterling, 1969). The same 5-bundle pattern has been found elsewhere in the Rosales (sensu Cronquist), indicating that it may be ancestral for the entire order. Connaraceae, the most recent addition to the list of 5-bundle families (Leinfellner, 1970; Dickison, 1971) now seems more at home in Cronquist's Rosales than in his Sapindales (see Cronquist, 1968: 264).

Much has been written on the supposed conservatism of floral vascular bundles, that is, on the idea that evolutionary changes in floral vasculature can lag behind changes in external form (see Rohweder, 1972; Schmid, 1972a). Recent opposition to the concept has been strong and well presented. Any floral anatomist who constructs a phylogenetic scheme based on vascular conservatism now needs good ancillary evidence if he wants to convince his colleagues. Nevertheless, I doubt that the last word has been uttered on this topic. In rebuking floral anatomists for ignoring the relationships between vascular structure and function, Carlquist (1969) emphasizes pollination and dispersal mechanisms. I do not know that any opponent or proponent of vascular conservatism has considered the possible role of bundles—as procambial strands—in floral morphogenesis. Tucker's (1961) investigations indicate that procambial strands in the upper receptacle of *Michelia* act as organizers, affecting the order of carpel initiation. If procambial strands are organizers, evolutionary processes might "conserve" some bundles because of their importance for the integrated development of the flower.

One recent advance in floral anatomy is the realization that the vascular system is much more variable in some taxa than in others and that the manner in which bundles interconnect may have more to do with the proximity of strands during floral development than with phylogeny (Tucker, 1966). Another is the realization that floral bundles do not always extend acropetally in





FIGURES 7–8.—7. Diagrammatic longitudinal section of a female *Nestronia* (*Darbya*) flower; redrawn from Smith & Smith (1942). Section passes through two dorsal bundles (d), through a sepal and stamen on one side, and between the sepals on the other. Bundles supplying sepal and stamen are labeled s and st, respectively; r = "recurrent bundles"; scl = sclerenchyma; b = blindly ending branches from the recurrent bundles. Note that the recurrent bundles also terminate blindly (arrow) below the flower.—8. Diagrammatic longitudinal section through flower of *Calycanthus*; redrawn from Dengler (1972). br = bract; c = carpel; st = stamens; sto = staminodes; t = tepals. Recurrent bundles end blindly (arrows), as in *Nestronia*.

continuity with previously formed vascular tissue (Arnal, 1946; Paterson, 1961; Sterling, 1973).

Isolated initiation and differentiation of inverted bundles—bundles with phloem to the inside and xylem to the outside—are particularly interesting because inverted floral bundles were once considered valuable indicators of ancestry. The inverted "recurrent" bundles in *Nestronia* (Fig. 7) and some of its relatives were supposed to show that the inferior ovary of Santalaceae is of receptacular origin, having evolved by "invagination of the floral axis and subsequent fusion of the resultant cup-shaped receptacle to the ovary" (Smith & Smith, 1942; see also Puri, 1952a; Douglas, 1957; Eames, 1961). This belief is incorporated in the diagram of relationships within the Santalales by Smith & Smith (1943).

Inverted bundles in the placental region of Capparales have inspired some of the more extreme interpretations in the field of floral anatomy. Puri, after a series

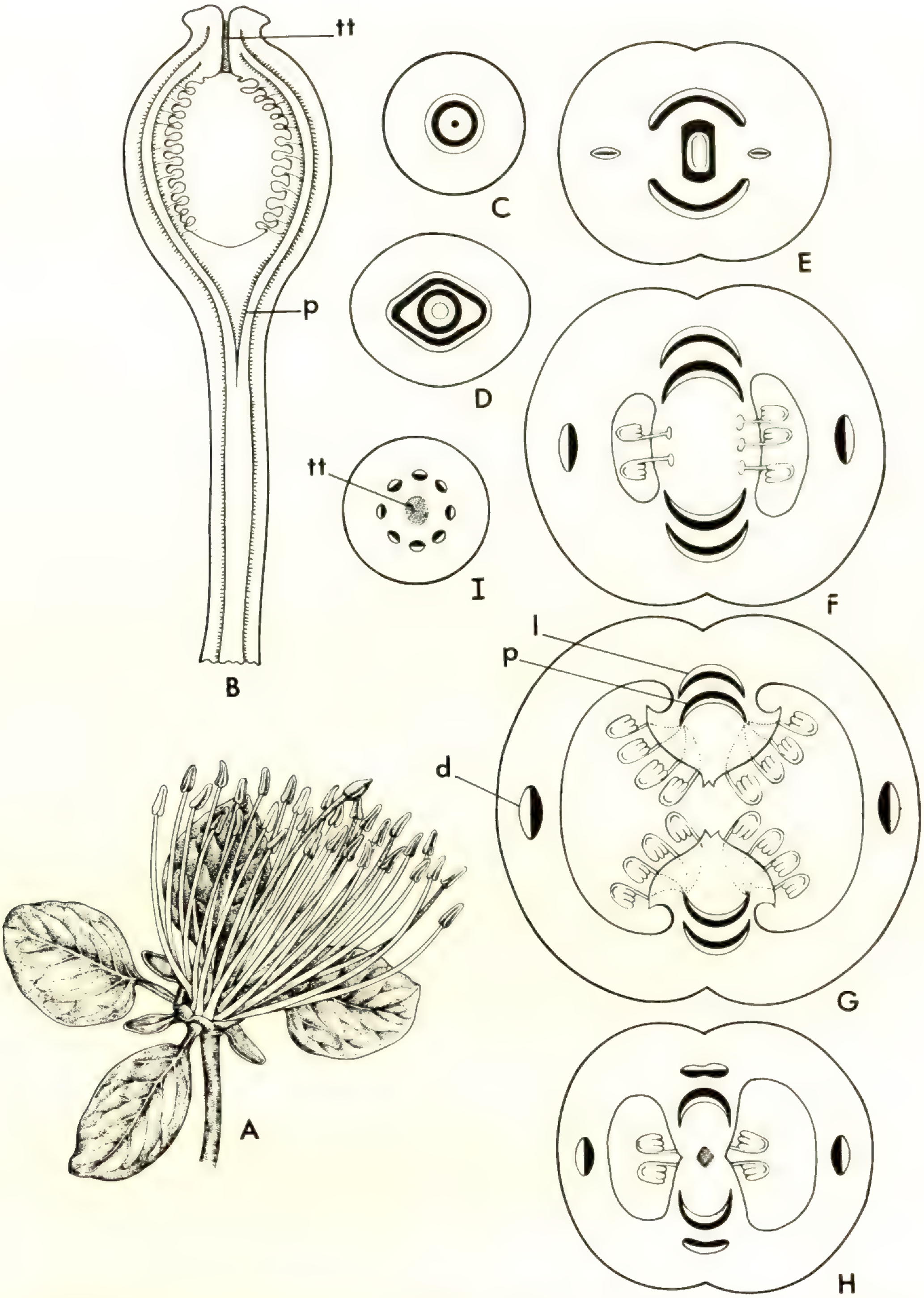


FIGURE 9. *Crataeva religiosa*.—A. Flower; redrawn from Brown (1938).—B. diagrammatic longitudinal section of gynoecium.—C–I. Diagrammatic cross sections of gynoecium from base upward showing arrangement of vascular tissue; redrawn from Puri (1950). d = dorsal bundle; l = lateral bundle; p = inverted, blindly ending placental bundles; tt = pollen-transmitting tissue.

of studies on the Capparales and certain families in the Violales, dismissed elaborate evolutionary schemes in favor of a simple explanation: "In the ancestors of these families the ovary had axile placentation—a condition still seen in certain species of the Capparidaceae, Passifloraceae and Cucurbitaceae. In a change from axile placentation to parietal the placental strands have shifted to the periphery, but they have still retained their inversion so characteristic of axile placentation. Thus, the inversion of these bundles is just a relic of past history which has somehow been retained" (Puri, 1952b).

Puri's explanation has been favorably received (Cronquist, 1968: 214; Carlquist, 1969: 335), and I do not doubt the shift from axile to parietal placentation; however, the evolution of the unique capparalean bundle arrangement may also have involved a change in morphogenetic control. I am led to this conjecture by Dengler's (1972) work on *Calycanthus*. Dengler found that the inverted "recurrent" bundles in the floral cup of *Calycanthus* (Fig. 8) are induced after intercalary growth has occurred and that these bundles are initially separate from the main vascular supply. The subsequent union with the main vascular supply is through a complicated set of anastomoses below the androecium (confirmed in conversation with Dengler).

The explanation for the inverted orientation of xylem and phloem in some floral bundles may lie in the initial isolation of these bundles. The xylem and phloem of normal acropetally extending bundles differentiate under the influence of the more mature vascular tissue with which they are in contact. Bundles starting as isolated strands are exposed to a different set of morphogenetic factors, and the controlling factor may then be the position of the xylem in the nearest maturing bundle running parallel and exterior to the isolated strand. (See Fisher, 1971, on the tendency of xylem poles to face one another.)

Puri (1950) has shown that the inverted placental bundles of *Crataeva* are not continuous with the rest of the vascular system at flowering time (Fig. 9). This may be an ancestral feature of the Capparaceae, linked in some way with the evolution of the long stalks (gynophores or androgynophores) that bear the ovaries in this family. In any case, it is not hard to believe that gynoecial vasculature so markedly isolated would be morphogenetically exceptional, especially when the isolation involves an extremely active intercalary meristem.

The cross-sections and descriptions of *Nestronia* by Smith & Smith (1942) suggest that here, also, the inverted bundles are initially separate from the main vascular supply.[6] As in *Calycanthus*, the inverted bundles join the normally oriented ascending bundles in a series of anastomoses beneath the stamens. There are no other significant connections between these two sets of bundles. The smooth curves from ascending bundles to recurrent bundles in diagrams that Smith & Smith (1942) and others (e.g. Fahn, 1974: 444) have based on *Nestronia* are largely poetic license. Recurrent bundles are poorly developed or lacking in some of the least specialized santalaceous flowers, e.g., those of *Henslowia* and *Choretrum*, which are perfect and have 5-merous, basally septate gynoecia

[6] Isolated development of the placental supply has been reported for a number of Santalaceae (Rao, 1942; Smith & Smith, 1943; Fagerlind, 1959).

(Smith & Smith, 1943; Raj, 1972). These bundles therefore appear to be a secondary evolutionary phenomenon, undeserving of the phylogenetic importance that the Smiths attributed to them.

Investigators who base phylogeny on floral vasculature are known to be imaginative and critical—imaginative when writing their own contributions, critical when evaluating someone else's. Progress in this peculiar field will be made by those who can combine their observations, both imaginatively and critically, with data from descriptive and experimental morphogenesis.

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THE BASES OF ANGIOSPERM PHYLOGENY: VEGETATIVE MORPHOLOGY[1]

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ABSTRACT

Coherent patterns of morphology of apparent value in determining taxonomic and phylogenetic relationships are present in dicotyledonous leaves. Features of greatest value in assessing these affinities include leaf organization; marginal features, including morphology of the tooth; major vein configuration; characters of the intercostal venation; and gland placement. Of these, recognition of tooth morphology appears to be an overlooked tool of major systematic importance. Variation in these features is most coherent when analyzed in terms of the Takhtajan and Cronquist systems of dicot classification. Essential to our procedure was a recognition of the "basic" leaf features of each taxon. These were regarded as the most generalized type from which all of the more specialized types in a taxon could have been derived and they were derived from an analysis of the comparative morphology of modern leaves with limited input from the fossil record. The resulting scheme indicates strong correlation of leaf features with six of the seven Takhtajan subclasses, in addition to paralleling and clarifying both systems at the ordinal and familial levels. Conspicuous exceptions are the breakdown of the Asteridae into a possible rosid and a possible dilleniid group, reassignment of the Celastrales and Myrtales to the Dilleniidae, and of the Juglandales to the Rosidae. Affinities of numerous problem taxa, such as the Didymelaceae and Medusagynaceae, are resolved, as are some of the points of disagreement between the Takhtajan and Cronquist arrangements. This analysis also provides the first systematic summary of dicot leaf architectural features and the outlines of a regular systematic method for leaf determination.

Inclusion of a paper dealing with vegetative morphology in a symposium on the Bases of Angiosperm Phylogeny may seem anomalous to many. Vegetative aspects such as branching patterns, phyllotaxy, growth form, leaf outline, and stem, bud, and root features have been extensively described and interpreted functionally and ontogenetically by workers such as Kerner (Kerner & Oliver, 1895), Goebel (1905), Troll (1967), and Radford et al. (1974). A limited systematic value has been recognized for vegetative features, especially within families and genera (see especially Hallé's work on the architecture of trees, Hallé & Oldeman, 1970; Hallé, 1971), and they have been used, usually as adjunct features, in the construction of taxonomic keys. However, no meaningful application has ever been made of vegetative morphology to the systematic consideration of angiosperms at the higher taxonomic levels.

Now our studies of modern and fossil angiosperm leaves indicate that coherent patterns of morphology of apparent value in determining taxonomic and phylogenetic relationships do exist among the leaves of the dicotyledons, and it is in order to elucidate these that we are making the following report. Because

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our experience has been restricted to leaves and because leaves appear to provide a far more abundant and varied set of characters than other vegetative organs, these will be the only features examined in this report.

The study of leaf morphology, particularly in its systematic applications, has been a regrettably neglected area of study by modern botanists. This was due in part to a belief in the plasticity of the leaf under a variety of environmental conditions and selective processes and to their possession of a seemingly bewildering array of features difficult to describe. As with other vegetative characters, some limited use was made of leaves in systematic studies and identifications at the familial and generic levels (especially Lam, 1925; Blackburn, 1952; Harrar & Harrar, 1962; Hutchinson, 1969; Preston, 1961; van Beusekom, 1971) but never at higher ranks.

Paleobotanists, on the other hand, have seldom been reluctant to claim that leaves can serve as the basis for angiosperm identification. A number of paleobotanical workers of the late nineteenth and early twentieth centuries, including von Ettingshausen, Saporta, Lesquereux, Hollick, Knowlton, Berry, and Chaney, based a major portion of their research on the identification of angiosperm leaf impressions. No systematic basis for such identifications was ever developed, and when they are critically examined, they are found to rest on gross morphological similarities in features such as leaf shape, principal vein course or marginal outline, or on superficial comparisons to modern herbarium specimens. The resulting volume of misidentifications is now so great that the validity of almost all paleobotanical identifications based on leaves is open to serious questions (Cronquist, 1968: 39–40; Penny, 1969; Hickey, 1971a; Wolfe, 1972; Hickey, 1973; Dilcher, 1974) and much of the previous work must be restudied. Another result of the "picture matching" (Wolfe, 1972, 1973) of extinct forms with fancied modern descendants is the supposed great antiquity of many angiosperm genera leading to a fixist view of the angiosperm record (Doyle & Hickey, in press). In addition, as Cronquist (1968: 6) notes, matching techniques applied to the fossil record cannot by themselves "provide new or independent information on the evolutionary diversification of a group, or on the transitions between groups; they merely document the existence of a particular group at some time in the past."

Any attempt to utilize the angiosperm leaf in systematic studies must rest on a careful description of its morphology. The first attempt to codify such a terminology for the description of leaves was that of the Austrian paleobotanist, Constantin von Ettingshausen, especially in his publications dated 1858 and 1861. Although he made no effort to discriminate between features which were of taxonomic value and those which were merely descriptive—a shortcoming hardly surprising in view of the pre-Darwinian mentality still prevailing at that time—he did provide the first logical sequence of terminology and a simple means of analyzing vein pattern by the description of vein courses. However, his system remained largely ignored by students of modern plants after that time. More recently there has been a revival of interest in von Ettingshausen's system resulting in the publication of two classifications of leaf architecture (Mouton, 1970; Hickey, 1973). Hickey's system, which considerably augmented the scope

of von Ettingshausen's terminology, attempted to formulate unambiguous and non-overlapping definitions for all terms and to analyze their taxonomic utility. It will be adopted as the terminological base for this paper.

Having developed a terminology capable of describing the variations found in the architecture of angiosperm leaves, the next step was to determine if some systematic variation in leaf features corresponding to the various taxonomic groupings could be ascertained. The fact that such patterns can be discerned even at higher levels and that they can be comprehended most clearly when analyzed in terms of the classification systems for the dicots developed by Takhtajan (1966, 1969) and Cronquist (1968) forms the subject of this report.

The objectives of this paper are thus to:

1. Ascertain the distribution of leaf architectural features in the dicotyledons in terms of the Takhtajan and Cronquist systems of classification;
2. Assemble a plausible systematic ranking and ultimately a phylogeny which incorporates leaf data;
3. Provide the basic data and organization for a synoptic leaf key to the dicots.

The term "leaf architecture" which appears throughout this report will be used in the sense of Hickey (1973) to denote the placement and form of those elements constituting the outward expression of leaf structure, including venation pattern, marginal configuration, leaf shape, and gland position. Architecture in this sense is that aspect of morphology which applies to the spatial configuration and coordination of those elements making up part of a plant without regard to histology, function, origin, or homology.

Finally, it must be stressed that in assembling the systematic survey which follows, evidence from floral morphology, pollen, embryology, and anatomy was evaluated in addition to that of leaves. While establishing the value of leaves as a systematic character, we recognize that they must be considered in conjunction with other morphological features.

LEAF ONTOGENY

Angiosperm leaves arise as lateral primordia left behind by the apical meristem of the plant axis. Development of the mature leaf occurs through the elongation and expansion of this primordium which proceeds in three overlapping phases. These start with apical growth which is followed by marginal expansion and finally by an intercalary phase (Esau, 1965; Kaplan, 1971, 1973; Pray, 1955, 1963). Each of these stages may be variously prolonged or shortened to produce the wide variety of leaf shapes occurring in the angiosperms. Intercalary growth is absent in fern leaves with open dichotomous venation (Pray, 1960, 1962) and at least in the only form with simple reticulate venation which has been studied (Hara, 1964; however, see Pray, 1960, 1962).

At an early stage, the leaf primordium can be divided into two regions, termed the upper leaf zone and the lower leaf zone (Kaplan, 1973). Kaplan (1971, 1973) has demonstrated that unifacial (radial) monocot and dicot leaves undergo a virtually identical ontogeny. In bifacial dicot leaves the lamina develops, in all

FIGURE 1. Leaf form.—A. Simple, unlobed; *Ulmus floridana* Chapm.; USA: Florida, *Standley 12989* (US); × 1.—B. Simple, palmately lobed; *Platanus glabrata* Fernald; Mexico: Coahuila, *Pringle 8319* (US); × 1.—C. Pinnately compound; *Carya glabra* Sweet; USA: Louisiana, *Stone 437* (US); × ½.—D. Palmately compound; *Cannabis sativa* L.; USA: Maryland, (USNM Paleobotany Coll. 2013); × ½. (All photographs by Mr. James P. Ferrigno, Division of Paleobotany, Smithsonian Institution.)

but rare cases, from the upper leaf primordium and the stipules and sheathing leaf base (if any) from the lower leaf primordium. The petiole is intercalated between the two zones as the latest mature structure to appear, and its elongation causes the emergence of the leaf from the bud (Esau, 1965; Kaplan 1971, 1973). In contrast, in all cases where development is known, the blade of bifacial monocot leaves develops from the lower leaf primordium which also gives rise to the petiole, the stipules, and the sheathing base. The upper leaf zone, when present, is a radial projection from the leaf apex called the *Vorläuferspitze* (Kaplan, 1973). This basic difference in leaf development between the monocots and dicots indicates that the blades of each represent convergences in form whose adult morphology cannot be compared (cf. Kaplan, 1973: 446). It was for this reason that the leaf architectural method of Hickey (1973) was restricted to the dicots.

Vein development in pinnate dicot leaves begins with formation of the midvein during apical growth. The secondaries develop progressively outward from the midvein during marginal growth (Esau, 1965; Pray, 1955, 1963; Slade, 1957). The tertiary and higher vein orders develop simultaneously and successively during intercalary growth of leaves having imperfect or well developed areolation (Pray, 1955, 1963; Slade, 1957). Vein endings appear to differentiate progressively from the vascular strands surrounding the areoles (Pray, 1955, 1963; Slade, 1957, 1959). In the one known case of the ontogeny of a leaf with imperfect areolation (*Aucuba* in the Cornaceae) tertiary and higher order vein development is progressive (Pray 1955, 1963). In the monocots and dicots the direction of vein development is acropetal for the primary and secondary veins and basipetal for the higher order vein network (Esau, 1965; Kaplan, 1973).

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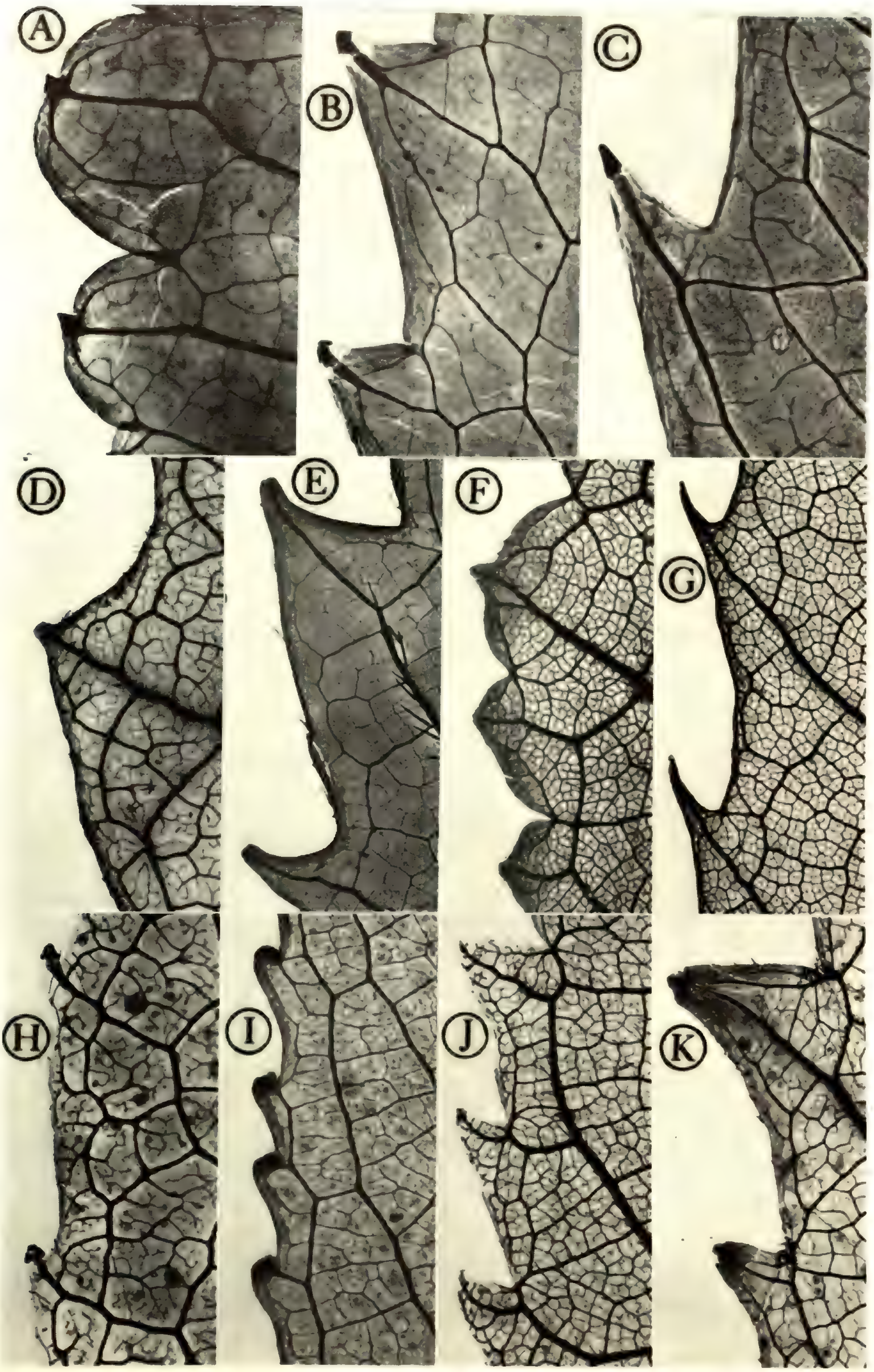
FIGURE 2. Some important tooth types; all × 7½.—A. Chloranthoid; *Chloranthus henryi* Hemsl. (Chloranthaceae); China: Yunnan, *Henry 9962* (US).—B. Chloranthoid; *Ascarina lucida* Hook. f. (Chloranthaceae); New Zealand: Moehan, *Cranwell & Moore s.n.* (US).—C. Monimioid; *Atherosperma moschatum* Labill. (Monimiaceae); Australia: *Hueber s.n.* (USNM Paleobotany Coll. 243).—D. Platanoid; *Fothergilla major* Lodd. (Hamamelidaceae); Ex Biltmore Herbarium 708g (US).—E. Platanoid; *Euptelea polyandra* Sieb. & Zucc. (Eupteleaceae); Japan: *Dorsett & Morse 543* (US).—F. Urticoid; *Corylus colurna* L. var. *chinensis* (Franch.) Burkill (Corylaceae); China: Yunnan, *Rock 4798* (US).—G. Spinose; *Castanea dentata* (Marsh) Borkh. (Fagaceae); USA: Rhode Island, *Bartlett 2681* (US).—H. Theoid; *Hartia sinensis* Dunn (Theaceae); Britain: cultivated, *Meyer 6031* (US).—I. Salicoid; *Salix fragilis* L. (Salicaceae); USA: Iowa, *Thorne 13312* (US).—J. Cunonioid; *Lamanonia* sp. aff. *speciosa* Camb. (Cunoniaceae); Brazil: São Paulo, *Fontella 137* (US).—K. Rosoid; *Ampelopsis brevipedunculata* (Maxim.) Frautre var. *heterophylla* (Thunb.) Hara (Vitaceae); Phillipines: Luzon, *Barnes 20191* (US).

FIGURE 3. Configuration of the principal veins of the leaf and gland position.

FIGURE 4. Orientation of intercostal venation; all × 10.—A. Random; *Degneria vitiensis* Bailey & A. C. Smith (Degneriaceae); Fiji: Viti Levu, *Smith 6301* (US).—B. Admedial; *Trimenia papuana* Ridley (Trimeniaceae); Papua: *Brass 23200* (US).—C. Reticulate; *Talauma angatensis* (Blanco) F. Vill. (Magnoliaceae); Philippines: *Williams 1354* (US).—D. Reticulate; *Exbucklandia populnea* (R. W. Br. ex Griff.) R. W. Br. (Hamamelidaceae); Sumatra: *Bartlett 8007* (US).—E. Transverse, irregularly percurrent; *Canarium pimila* Kon. (Burseraceae); China: *Morse 318* (US).—F. Transverse, regularly and strongly percurrent; *Corylus chinensis* Franch. (Corylaceae); China: Hupeh, *Wilson 2280* (US).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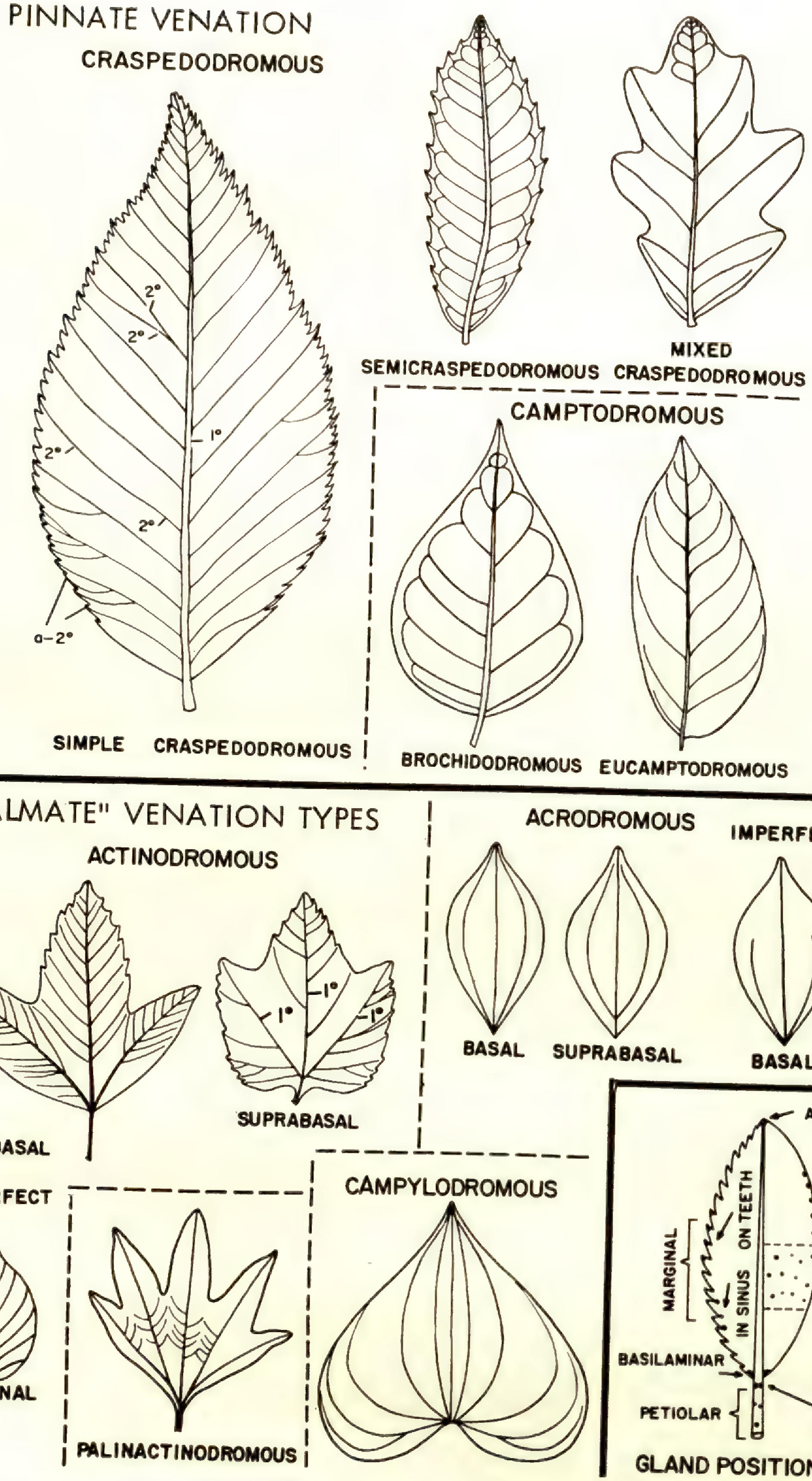
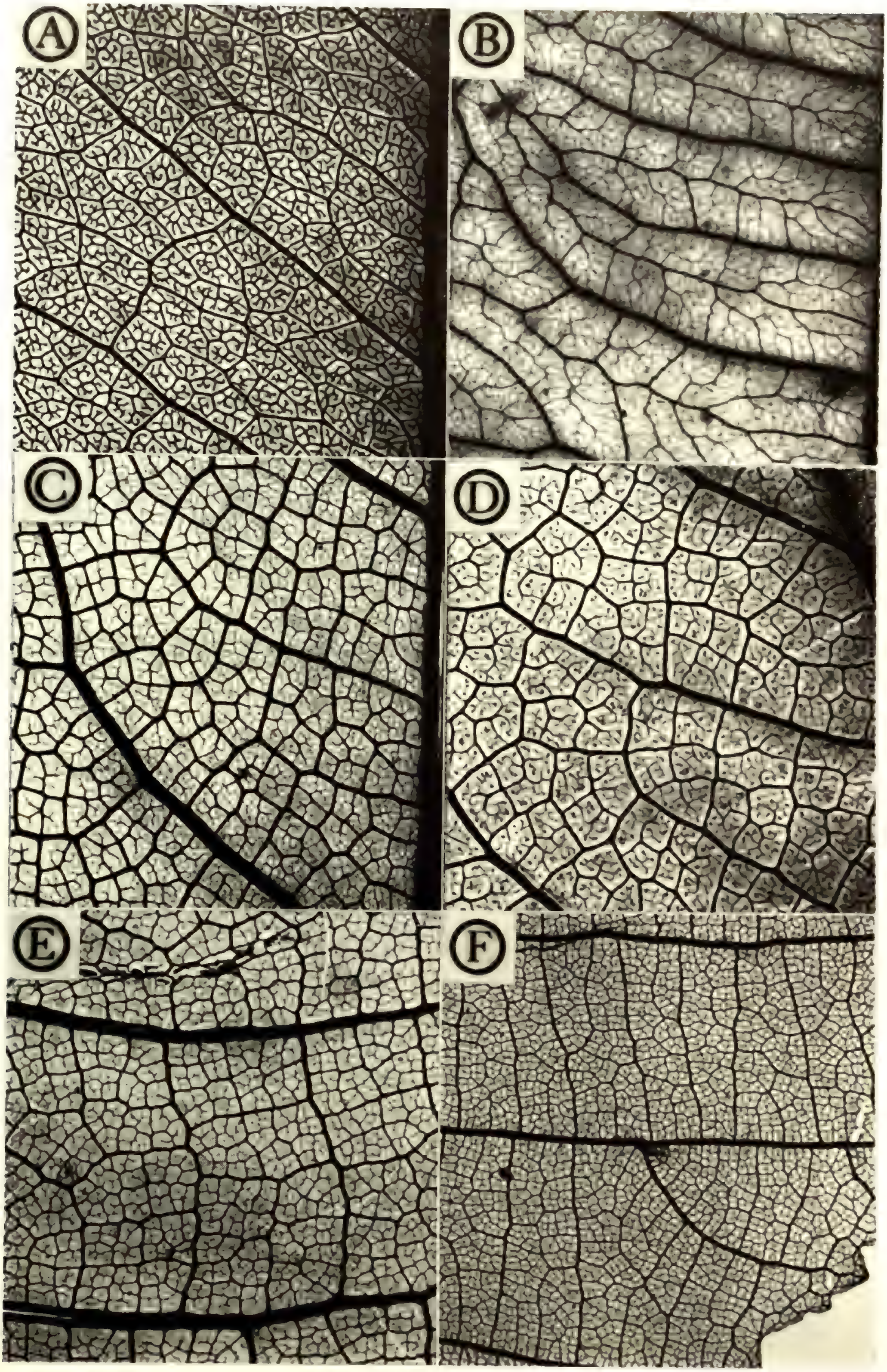

PINNATE VENATION
CRASPEDODROMOUS
2°
2°
1°
2°
2°
a–2°
SIMPLE CRASPEDODROMOUS
SEMICRASPEDODROMOUS
MIXED CRASPEDODROMOUS
CAMPTODROMOUS
BROCHIDODROMOUS
EUCAMPTODROMOUS
"PALMATE" VENATION TYPES
ACTINODROMOUS
1°
1°
1°
BASAL
SUPRABASAL
IMPERFECT
MARGINAL
PALINACTINODROMOUS
CAMPYLODROMOUS
ACRODROMOUS
BASAL
SUPRABASAL
IMPERFECT
BASAL
APICAL
MARGINAL
IN SINUS ON TEETH
MARGINAL
LAMINAR
MARGINAL
BASILAMINAR
PETIOLAR
ACROPETIOLAR
GLAND POSITION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FEATURES OF ANGIOSPERM LEAVES

Despite their different modes of ontogeny, both monocot and dicot leaves possess certain common features whereby they can be recognized as angiospermous. None of the characters in the list below are universally present, but the presence of one or more of them is strong evidence of angiospermy. They are:

1. Intercalary growth as the major phase of blade expansion.
2. Stipules. These are frequently absent in the dicots and rare in the monocots where they occur in the Hydrocharitaceae, Butomaceae, Najadaceae, and several other families.
3. Several discrete orders of venation. Almost always three and usually four or more but highly reduced leaves may have fewer than three orders of venation.
4. Freely ending veinlets. Not always present.
5. Vein anastomoses between two or more orders of veins. Not always present but, when so, diagnostic of the angiosperms.

Characteristic features of monocot blades are their development from the lower leaf primordium, a preponderance of parallel venation, and a strong tendency for the longitudinal secondary venation to converge at the leaf apex (Doyle, 1973). Dicot laminas develop from the upper leaf primordium, have a strong tendency toward reticulate venation, and show a predominance of leaves having pinnate venation.

We base our survey of dicot leaf architecture on over ten years of study of the great majority of dicot families from cleared leaves and herbaria collections. Our coverage has been particularly complete in the subclasses Magnoliidae, Ranunculidae, Dilleniidae, Hamamelididae, and Rosidae. At the present time, cleared and stained leaves in the U.S. Geological Survey collection at Menlo Park, California, number approximately 10,500 species and that of the Smithsonian Division of Paleobotany approximately 2,250 species. These specimens were prepared using the method of Foster (1952) modified by Hickey (1973). Taxonomic and collection data on the many tens of thousands of specimens either surveyed or examined in detail in order to complete our review of dicot leaf architectural features are far too voluminous to supply here.

Architectural features of greatest importance in assessing systematic and phylogenetic affinities at the higher taxonomic levels are listed below. These are:

1. Simple versus compound organization (Fig. 1).
2. Entire versus toothed margins.
3. Characteristics of the tooth including shape, characteristics of the apex, occurrence and type of glandular processes, and vein configuration within the tooth (Figs. 2–3).
4. Major vein configuration, e.g., pinnate, actinodromous; secondaries craspedodromous, camptodromous, etc. (Fig. 3).
5. Characteristics of the intercostal venation including its orientation, and the presence and type of intersecondaries (Figs. 4–6).
6. Gland position, including marginal, laminar, acropetiolar, etc. (Fig. 3).

FIGURE 5. Leaves showing intersecondary veins between secondaries. In addition, A is "festooned brochidodromous," that is, it has a set of secondary loops outside of the main brochidodromous arch.—A. *Ternstroemia tepazapote* Cham. & Schlecht. (Theaceae); Belize: *Gentle 3838* (US).—B. *Pseudoxandra coriacea* R. E. Fries (Annonaceae); Brazil: Terr. Amazonas, *Wurdack & Addersley 43492* (US). Both × 1.

These terms and ones related to them will recur frequently in the detailed descriptions and are fully defined by Hickey (1973, in press). Description of tooth types, which proved to be a major systematic tool in this survey, will be a part of the description of the subclass in which they occur. Further definitions of tooth descriptive terms may be consulted in Hickey (in press).

PROCEDURES

In the summaries which follow we will use the classifications of Takhtajan (1966, 1969) and Cronquist (1968) as the systematic framework for presenting our data on leaf architectural variation. We found these systems to yield the most coherent arrangement of foliar features. We supplemented this with data from other systems, particularly from those of Thorne (1968) and Airy Shaw (1966), where we felt that this was warranted. If evidence from foliar morphology indicated that a particular family or order had been misplaced, especially if this was supported by other features, we described it where its foliar features suggested that it fit better. In a number of cases leaf architecture helps to resolve areas of disagreement between Takhtajan and Cronquist, e.g., leaf data support Takhtajan's assignment of the Euphorbiaceae to the subclass Dilleniidae, while Cronquist appears to have been correct in excluding the Lecythidaceae from the subclass Rosidae.

We also tried to establish the "basic" leaf features for each of the taxa from

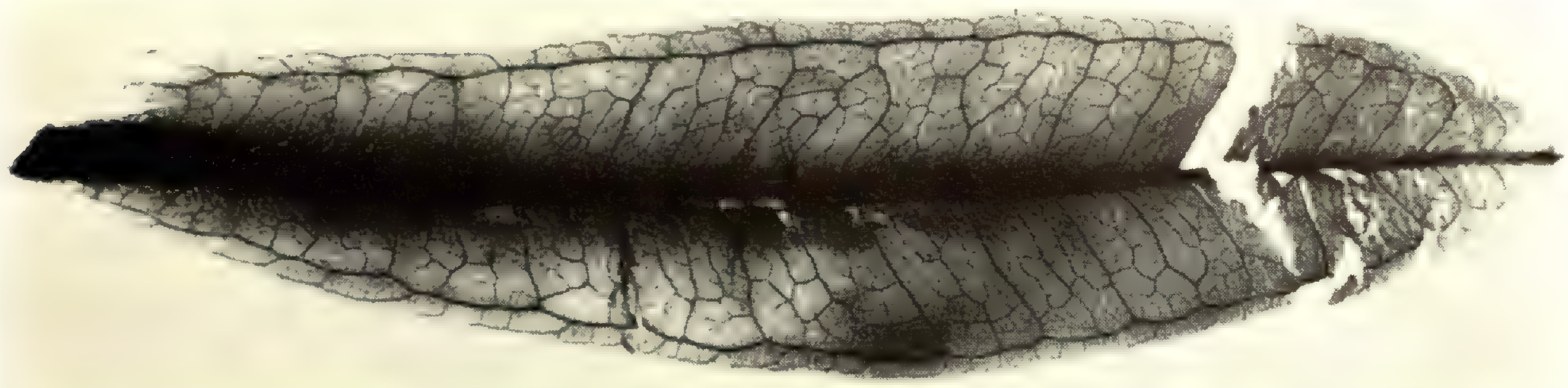

FIGURE 6. Intramarginal vein in *Hibbertia ebracteata* Bur. ex Guillaum. (Dilleniaceae); New Caledonia: M. des Sources, *McKee 2097* (US); × 1. Such veins are inferred to form by the fusion and strengthening of the secondary vein segments forming the brochidodromous arch.

subclass through order and in some cases to the level of family. Our concept of basic features are those that serve as the most general types from which all the more specialized types occurring within a taxon could have been derived. These basic characters are not necessarily the most primitive that ever occurred within the taxon. Such features may have been markedly unsuccessful in the long run but were able to give rise to the basic set which then underwent radiation and diversification.

In the following summary of basic characters of the various taxa, especially for the subclasses, we have included only those about which we could make a judgment. Our designation of a character as basic was reached by application of the six criteria listed below, of which only the relatively scanty contribution from the fossil record could be considered as conclusive evidence, rather than merely indicative.

The criteria are:

1. The fossil record.
2. Features possessed by the most primitive living member(s) of a taxon.
3. Features possessed by a number of taxa that are related to the one being analyzed either as ancestors, direct descendants, or as common descendants.
4. Features possessed by the most primitive members of a number of subdivisions of the taxon under examination.
5. The presence, even in only a few forms of a taxon, of a feature considered irreversibly lost, such as a characteristic tooth type.
6. A hypothetical combination of features needed to reconcile a number of trends considered divergent from a common ancestor.

As an example of our reasoning, after applying these criteria to a summary of basic characters in the subclass Ranunculidae, we could reach no judgment as to the status of latex. Thus, mention of this character was excluded from the description of the subclass.

The concept of what constitute the basic features of a taxon has permitted us to assemble the summary which follows. It is organized so that it can be used in a synoptic way to systematically determine the higher level affinities of unknown leaves. This is especially so in the case of the diagrams representing groupings

TABLE 1. Primitive versus advanced features of dicotyledonous leaves. Fossil evidence is available for items 1 through 5 only. (From Doyle & Hickey, in press.)

Primitive	Advanced
1. Leaves simple	1. Leaves compound
2. Pinnate venation	2. Other configurations
3. Secondaries camptodromous	3. Other configurations
4. First rank level of vein organization	4. Higher ranks
5. Margin entire	5. Margin toothed or lobate
6. Stipules present	6. Stipules absent

of leaf characters in the various subclasses where a number of probable convergences in leaf architecture may have been grouped together. This arrangement was maintained because it represents a coherent grouping of characters facilitating leaf identification, and not because it necessarily represents an accurate picture of dicot phylogeny.

Although data from the fossil record are still rare, they did provide some assistance in determining which leaf architectural features are primitive and which are advanced (summarized in Table 1). In certain cases this allowed general trends within subclasses to be established on grounds other than modern comparative morphology. Evidence that items one through five of Table 1 represent primitive character states for dicot leaves is derived from studies of the earliest known fossil angiosperm leaf assemblages which occur in the probable early Aptian Stage of the Cretaceous Period (Doyle & Hickey, in press). These leaves are all simple with pinnate venation and irregularly brochidodromous secondary veins forming a set of loops that do not intersect the leaf margin. These authors (Hickey & Doyle, 1972; Doyle & Hickey, in press) also described a trend in which the earliest angiosperm leaf fossils have all of their vein orders poorly differentiated from one another and are irregular in their courses, manner of branching, and anastomoses. These features are associated with decurrency of secondary veins, irregularly shaped intercostal areas, and often with poor separation of blade and petiole. From this "first rank" stage, Albian-early Cenomanian leaves show a gradual increase in vein differentiation and regularity of course and spacing at progressively higher orders of venation. This pattern coincides with a general trend for increase in leaf rank with supposed phylogenetic advancement in modern leaves found by Hickey (1971b) and was an aid in corroborating our surmises as to advancement at the ordinal and familial levels.

Fossil evidence for point five in Table 1 is somewhat less certain since two rare serrate forms are found even in the lowest level of angiosperm leaf occurrence. However, these fossil leaves are not diverse in tooth shape or form and they occur among a far more diverse and abundant group of entire-margin leaves. In our opinion, these facts argue for the more recent origin of serrate types.

The evolutionary status of stipules is unclear since fossil evidence is lacking and evidence from comparative morphology is subject to conflicting interpretations. However, their presence in both monocots and dicots (Eames, 1961; Sinnott & Bailey, 1914), their common association with the more primitive dicot

families, and their generally vestigial nature lead us to the conclusion that they are in the process of phylogenetic reduction (Cronquist, 1968) and seem to indicate that stipules are primitive. Controversy over stipules necessarily involves the question of which type of nodal anatomy is primitive, inasmuch as stipules are found in association with tri- or multilacunar nodes (Sinnott & Bailey, 1914), whereas in their rare occurrences in unilacunar families, they are mainly scarious or minute.

Rather than reviving the controversy, we simply adopted as a general operating principle the condition that we would derive no stipulate, multilacunar group from an exstipulate taxon. We felt that the status of unilacunar stipulate leaves was unclear, as in the case of a stipulate species of *Garcinia* in the typically exstipulate family Guttiferae. Since all the characters of the inflorescence and foliar morphology of *Garcinia* are advanced, stipules may represent either a survival or a secondary acquisition.

SUMMARY OF LEAF FEATURES

In the following sections descriptions of dicot leaf architecture are carried to the level of orders where information is available. Important leaf trends or specializations manifested by particular families are also included, but an overall survey at familial level is beyond the scope of this paper and will be dealt with in a later publication.

Again it must be emphasized that the basic framework of ordinal relationships within and to the seven dicot subclasses is that of Takhtajan and Cronquist, with modifications as indicated from leaf architecture and other references. The listing of orders and especially the charts of leaf architectural relationships thus developed are not meant to be interpreted in a phylogenetic sense but to serve as visual schemes which allow an initial approach to be made in placing an unidentified leaf in a subclass and order. Despite the fact that evidence from as many organs as possible was evaluated, in addition to the Takhtajan and Cronquist systems, in arriving at these groupings, there is little doubt that some of the leaf architectural relationships we recognize are artificial. However, as the diagrams are meant to illustrate these leaf architectural relationships, we feel that they are satisfactory.

For purposes of comparison, Takhtajan's (1969) numbers for the orders have been retained throughout this summary, even where leaf architectural or other data indicate a change in the placement of the orders.

The following synoptic key to the subclasses of the dicotyledons is designed as a conceptual aid in visualizing their leaf features and not primarily as an identification tool. The entries are necessarily generalized and exceptions have been minimized or disregarded.

LEAF KEY TO THE DICOT SUBCLASSES

a. Leaf basically simple or, if compound, then palmately compound; latex occasionally present.
  b. Margin basically entire.
    c. Third and higher order venation mostly well developed and staining well with Safranin O; leaves of normal texture.

d. Primary venation basically pinnate, becoming perfect acrodromous, actinodromous, or campylodromous; secondaries festooned brochidodromous (i.e., looping in several orders, Fig. 5) to simple brochidodromous, to eucamptodromous; intramarginal veins absent (Fig. 6); intercostal venation random, reticulate, or percurrent; latex present only in the aquatic order Nymphaeales ---------- A. MAGNOLIIDAE (in part)

dd. Primary venation basically pinnate, becoming imperfect acrodromous; secondaries basically strongly brochidodromous and often forming an intramarginal vein (Fig. 6); intercostal venation often oriented parallel to the secondaries; latex common ----------G(I). DILLENIID-LEAFED ASTERIDAE

cc. Third and higher order venation mostly poorly developed and staining poorly with Safranin O; leaf texture often thick, fleshy, or mealy -- D. CARYOPHYLLIDAE

bb. Margin basically toothed.

e. Leaves basically pinnately veined with secondaries not congested toward the base; lamina never palmately compound.

f. Leaf margin with Chloranthoid or Monimioid Teeth (Fig. 2); intramarginal vein lacking; latex absent ---------- A. MAGNOLIIDAE (in part)

ff. Leaf margin with Dillenioid, Theoid, or Spinose Teeth (Fig. 2); intramarginal vein sometimes present; latex widespread ---------- E. PINNATE DILLENIIDAE

ee. Leaves basically palmately veined or, if pinnate, with secondaries congested toward the leaf base; lamina sometimes palmately compound.

g. Leaf margin with Chloranthoid, Platanoid, or Urticoid Teeth (Fig. 2) or their presumed derivatives; primary venation either actinodromous or palinactinodromous; tertiaries percurrent but not tending to become concentrically oriented with respect to the top of the petiole; latex absent ---- C. HAMAMELIDIDAE

gg. Leaf margin with Theoid Teeth or their presumed derivatives (Figs. 2, 15); primary venation perfect or imperfect actinodromous or its derivatives; tertiaries transverse, tending to become concentrically oriented with respect to the top of the petiole; latex often present ---- E. PALMATE DILLENIIDAE

aa. Leaf basically pinnately compound; latex absent.

h. Leaf form basically ternately pinnately compound, with ternately forking primary and secondary venation; or if simple, then with a fimbrial vein; leaf margin with Chloranthoid Teeth or their derivatives ---------- B. RANUNCULIDAE

hh. Leaf form basically pinnately compound, not ternate, also palmate or palmately lobed by compression of the rachis; if simple, without a fimbrial vein; leaf margin with Cunonioid Teeth (Fig. 2) or their derivatives ---------- F. ROSIDAE and G(II). ROSID-LEAFED ASTERIDAE

Summary of Dicot Leaf Features

SUBCLASS A. MAGNOLIIDAE

Leaves simple; margin basically entire; venation pinnate; secondary veins basically festooned brochidodromous (i.e., with several orders of marginal loops, Fig. 5A); intersecondary veins common; tertiary venation grading from random to reticulate and transverse; glands none; stipulate; latex present only in the Nymphaeales (Fig. 7).

Trends: 1. Breakdown of primitively pinnate venation (Doyle & Hickey, in press) to acrodromous in the Laurales and Piperales, campylodromous in the Aristolochiales, and actinodromous in the Nelumbonales. 2. Teeth in the Laurales, Chloranthaceae, and Illiciales. 3. Loss of intersecondary veins. 4. Transverse intercostal venation. 5. Loss of stipules.

The Illiciales are brought within this subclass on the basis of their nodes, simple leaves, and brochidodromous venation. These characteristics make the order anomalous for the Ranunculidae, in which it was placed by Takhtajan. In

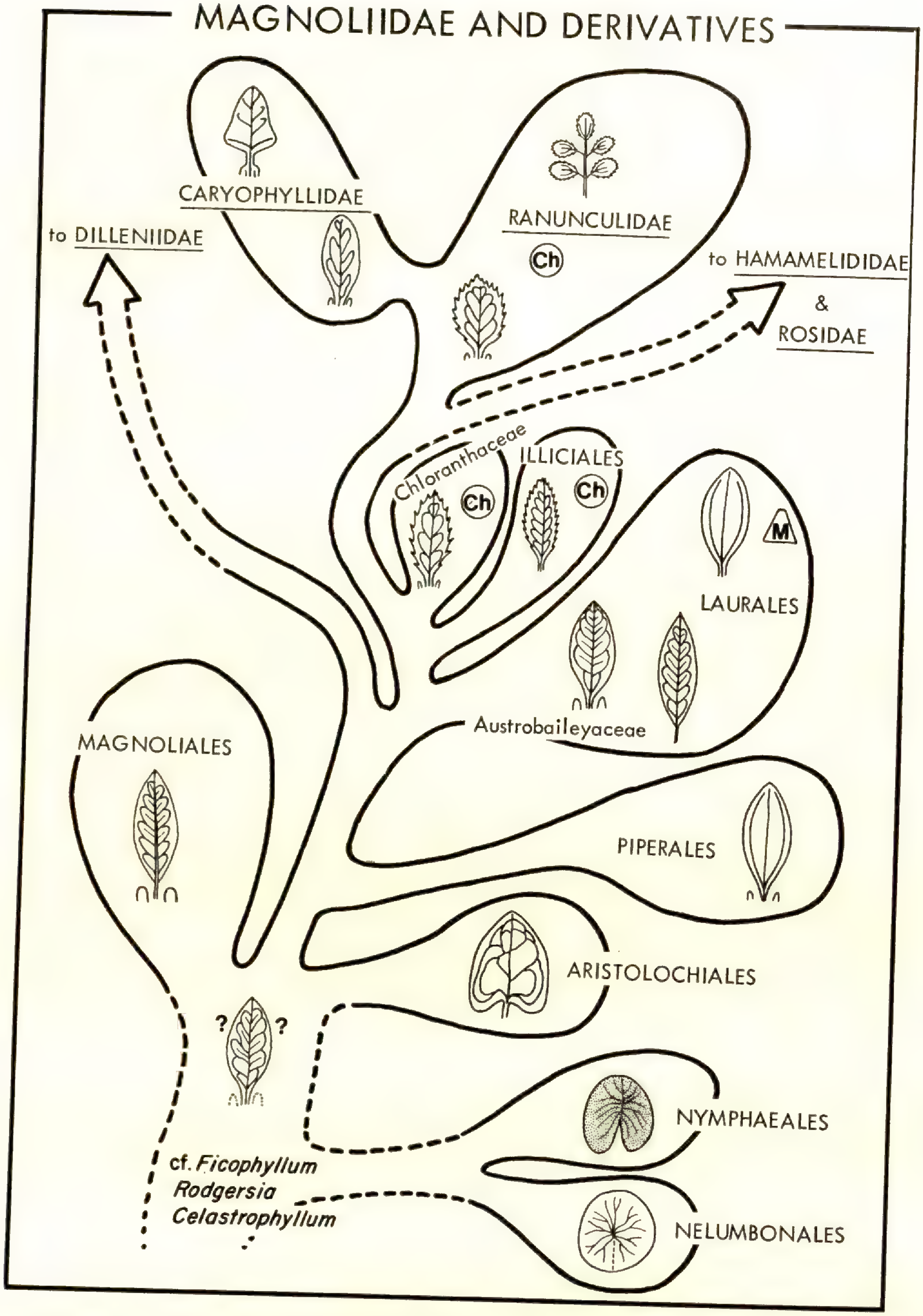

FIGURE 7. Leaf affinities in the Magnoliidae and derivatives. In this and the following affinity diagrams, positions represent morphological relationships which may or may not have a phylogenetic basis. The Takhtajan subclasses are underlined; taxa having latex are indicated by stippled leaves. Taxa having toothed leaves and the type of tooth are indicated by the

addition, the Nelumbonales are also brought within the subclass as an order more advanced than, but related to, the Nymphaeales. Inclusion of these forms with tricolpate pollen within the subclass assumes that this condition has arisen in separate lines of the dicots (see Muller, 1970: fig. 1; Walker, 1974).

Order 1. Magnoliales

Leaves simple; margin entire; venation pinnate; secondary veins festooned brochidodromous; intersecondary veins present; tertiary venation random, reticulate to transverse; stipulate.

Trends: 1. To eucamptodromy. 2. Disorganized to regular venation. 3. Loss of stipules in all families but the Magnoliaceae.

Order 2. Laurales (excluding Chloranthaceae)

Leaves simple; margin entire; venation pinnate; secondary veins brochidodromous with basal ones originating at a lower angle than those above; intersecondary veins common; tertiary venation reticulate to transverse; stipulate.

Trends: 1. Development of the Monimioid Tooth (Fig. 8 and defined below) having an unbraced medial vein; found in the Monimiaceae and the Trimeniaceae. 2. Secondaries originating at a uniform angle in the Monimiaceae, most Trimeniaceae, Lactoridaceae, Calycanthaceae, and Idiospermaceae. 3. To acrodromous venation in Amborellaceae, Hernandiaceae, and some Lauraceae. 4. To exstipulate in all families but Austrobaileyaceae and Lactoridaceae.

Family 15. Chloranthaceae

Leaves simple; margin with Chloranthoid Teeth having a medial vein "braced" by two prominent laterals which join it (Fig. 8); venation pinnate; secondary veins basically semicraspedodromous; tertiary venation random, reticulate to weakly transverse; venation staining poorly in Safranin O; stipulate.

Howard (1970, 1974) has shown that Swamy (1953) was incorrect in classifying the nodes of *Sarcandra* and *Chloranthus* as "modified unilacunar." In reality, leaves in these genera each have three gaps, with the two lateral gaps shared with the opposite leaf of the pair. The trace arising from these lateral gaps is also shared or "split," forking above its origin and sending a girdling bundle through the cortex into the marginal portion of both leaves. Howard classified these "split lateral nodes" as a new type but showed their close association with families and genera having the trilacunar condition. We think that this gap clearly arises from the standard trilacunar type in certain plants having opposite leaves and should most appropriately be considered as a modification of that type, termed perhaps the "shared trilacunar gap." Presence of these modified trilacunar gaps in the Chloranthaceae make it anomalous for the Laurales. In addition, if the Chloranthoid Tooth, which the family shares with the trilacunar ranunculids and Trochodendrales and with the unilacunar Illiciales,

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←

symbol shape and the letter within the symbol. M = Monimioid; Ch = Chloranthoid. Possible affinity with the Lower Cretaceous fossil genera *Ficophyllum*, *Rodgersia*, and *Celastrophyllum* is indicated by question marks.

originated only once, and if the trend to unilacunar nodes is irreversible, then Chloranthaceae should be derived from trilacunar stock having Chloranthoid Teeth and would not be closely related to the basically entire-margined Laurales, where an entirely different tooth type—the Monimioid—developed in two families.

Order 7. Illiciales

Leaves simple; margin with Chloranthoid Teeth; venation pinnate; secondary veins brochidodromous; tertiary venation random to reticulate or transverse; staining poorly in Safranin O; glands lacking; exstipulate.

Trends: Loss of teeth in the Illiciaceae except in *Illicium anisatum*.

Order 3. Piperales

Leaves simple; margin entire; venation acrodromous; stipulate. Highly disorganized venation is found in the herbaceous family Saururaceae.

Order 4. Aristolochiales

Leaves simple; margin entire; venation acrodromous; exstipulate.

Trends: The acrodromous venation of *Saruma* and *Asarum* becomes campylodromous in *Aristolochia* with a corresponding increase in vein regularity and leaf rank.

Order 6. Nymphaeales

Leaves simple, deeply lobed at the base with the margin reaching the centrally placed petiolar attachment; margin entire; venation essentially pinnate with the secondary veins strengthened and radiating actinodromously; latex present.

Order 8. Nelumbonales

Leaves simple, truly peltate by apparent fusion of the basal lobes along a line of suture; margin entire; venation truly actinodromous with numerous primaries; latex absent.

Despite its tricolpate pollen, this order is placed after its apparent nearest relative in the Magnoliales rather than in the Ranunculidae.

Magnoliid Tooth Types

1. *Chloranthoid*—Ch (Figs. 2, 8)—Chloranthaceae, Illiciales. Glandular; with a clear, non-deciduous (i.e., papillate) swollen cap, shape variable, acumi-

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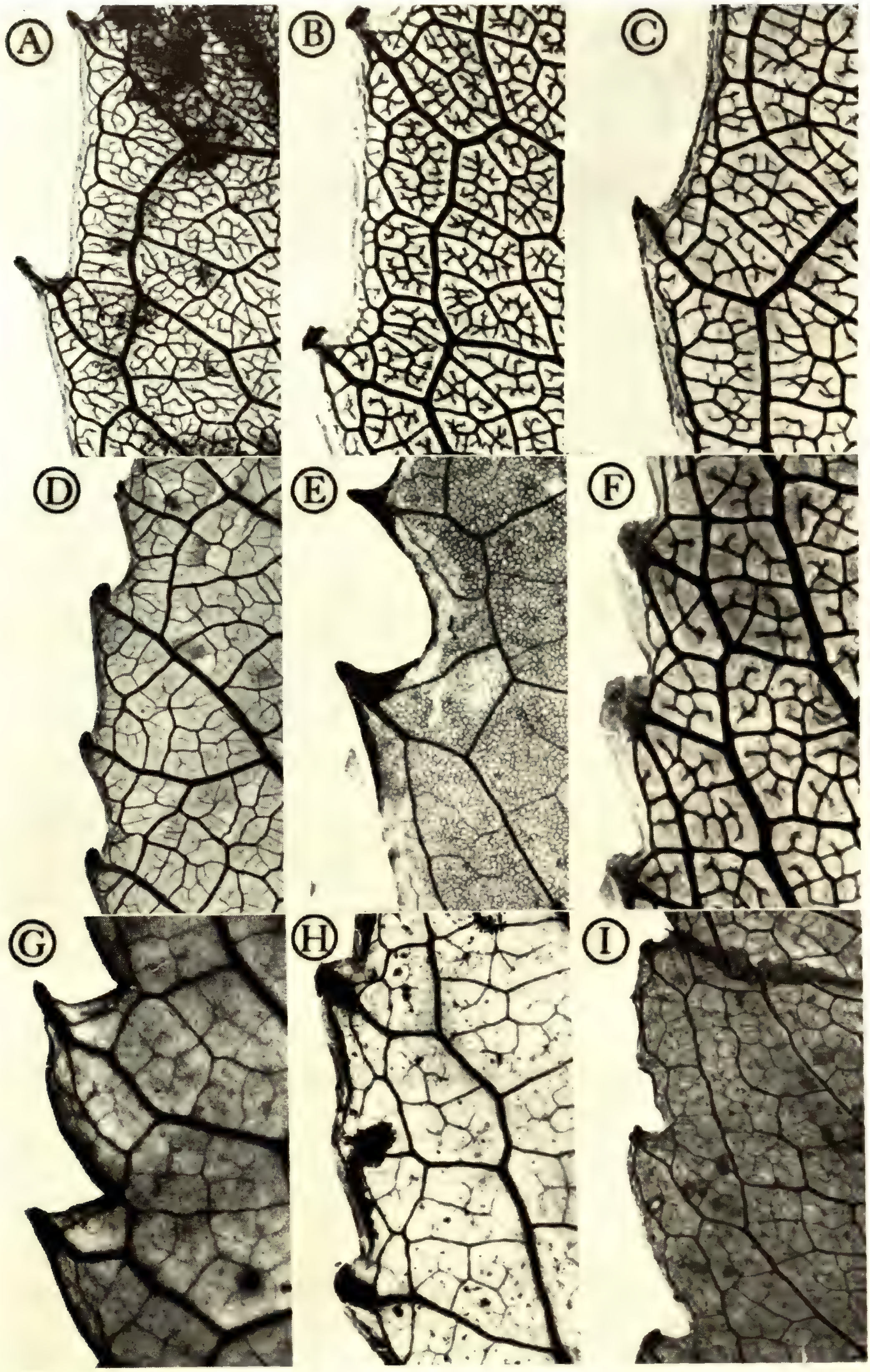
FIGURE 8. Tooth types and their variation in the Magnoliidae; all × 7½.—A–D. Monimioid.—A. *Mollinedia elegans* Tul. (Monimiaceae); Brazil: São Paulo, *Hancho 2067* (US).—B. *Macropeplus ligustrinus* (Tul.) Perk. (Monimiaceae); Brazil: Rio de Janeiro, *Glaziou 11991* (US).—C. *Hedycarya arborea* Forst. (Monimiaceae); New Zealand: Bay of Islands, *Wilkes s.n.* (US).—D. *Trimenia* sp. (Trimeniaceae); Africa: *Mundt & Marne s.n.* (US).—E–I. Chloranthoid; all Chloranthaceae.—E. *Sarcandra glabra* (Thunb.) Nakai; Okinawa: *Conores 1158* (US).—F. *Hedyosmum* cf. *glaucum* Solms; Peru: Huambos, *Souksup 4472* (US).—G. *Chloranthus serratus* Roem. & Schultz; Japan: Feyiyama, *Dorsett & Morse 503* (US).—H. *Chloranthus officinalis* Blume; Thailand: Nan Province, *Walker 7994* (US).—I. *Hedyosmum artocarpus* Solms.; Mexico: Cuernavaca, *Pringle s.n.* (US).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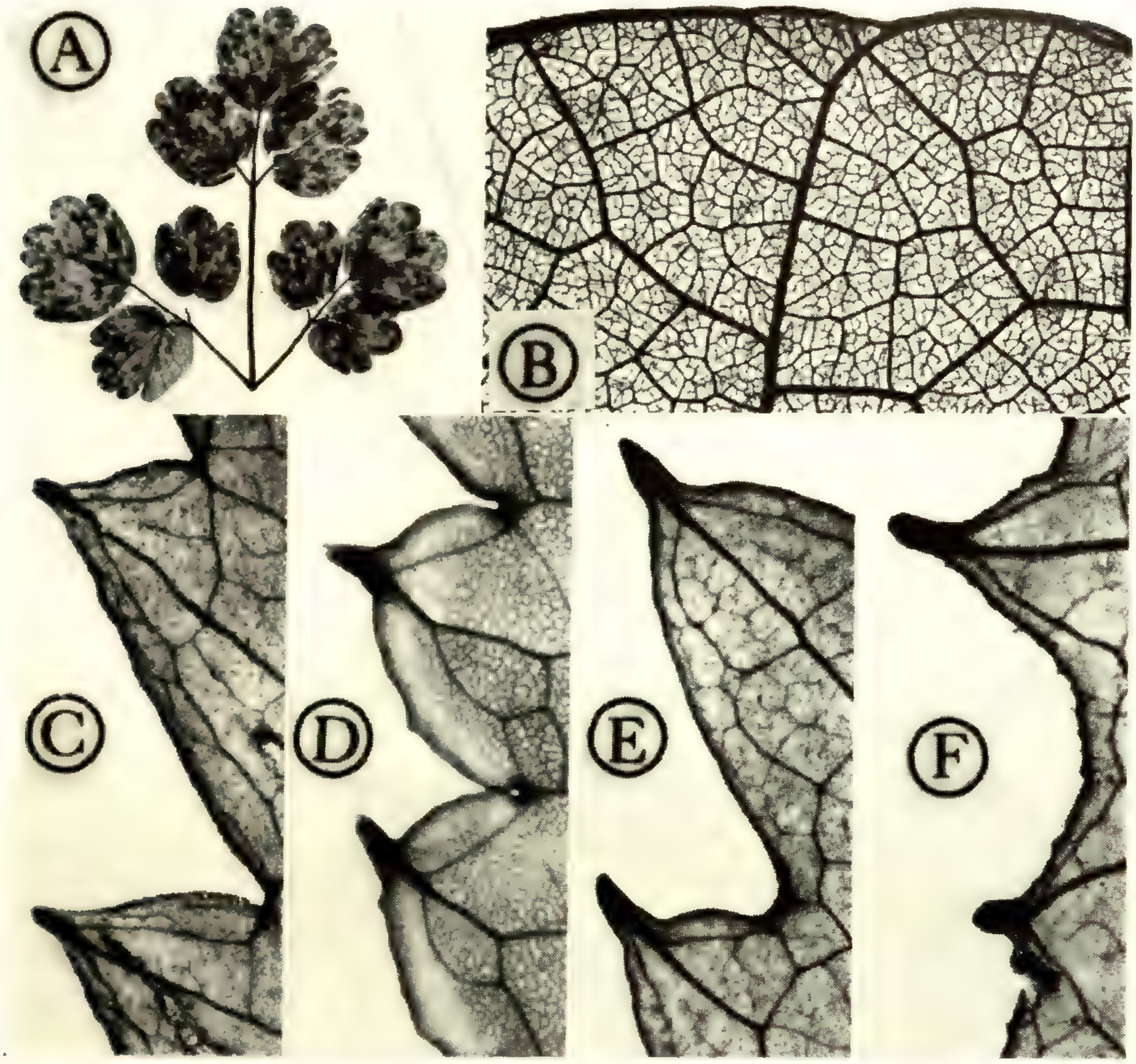


FIGURE 9. Leaf features of the Ranunculidae.—A. Portion of a ternate pinnately compound leaf; *Thalictrum dioicum* L. (Ranunculaceae); USA: Michigan, *Chandler s.n.* (US); × 1.—B. Fimbrial vein; *Cyclea polypetala* Dunn (Menispermaceae); China: *Henry 11979A* (US); × 5.—C–F. Chloranthoid Teeth; all × 10.—C. *Actaea pachypoda* Ell. (Ranunculaceae); USA: Virginia, *Palmer & King 76* (US).—D. *Beesia calthaefolia* (Maxim.) Ulbr. (Ranunculaceae); China: Hupeh, *Wilson 1292* (US).—E. *Podophyllum emodi* Wall. (Podophyllaceae); Pakistan: Punjab Province, *Rodin 5353* (US).—F. *Diphylleia grayi* F. Schmidt (Podophyllaceae); Japan: Shinano, *Collector Unknown* (US 205563).

nate-convex is common, acuminate-acuminate and concave-acuminate also occur. Venation with a medial secondary or tertiary vein accompanied by two prominent, converging, higher order lateral veins which also enter the tooth apex or fuse with the medial vein below the apex. Occasionally, as in *Ascarina*, one of the converging laterals is suppressed.

2. *Monimioid*—M (Figs. 2, 8)—Monimiaceae, Trimeniaceae. With an opaque, non-deciduous glandular cap (i.e., cassidate) having an acute apex; tooth shape generally acuminate-convex; venation with a secondary or tertiary entering the tooth medially and not joined by lateral veins.

SUBCLASS B. RANUNCULIDAE

Leaves basically pinnately compound by ternate forking of the rachis (Fig. 9); margin with Chloranthoid Teeth; venation pinnate, forking ternately; secondary

veins craspedodromous; tertiary venation random, reticulate, transverse; glands none; stipulate (Fig. 7).

Trends: 1. To simple leaves in the Ranunculales. 2. Exstipulate in all but a few Ranunculaceae.

Order 9. Ranunculales

Leaves basically pinnately compound by ternate forking of the rachis; margin with Chloranthoid Teeth; venation craspedodromous with opposite secondaries; stipulate; latex absent.

Trends: 1. Leaves pinnately compound, as in some Lardizabalaceae, Sargentodoxaceae, and many Ranunculaceae, with a trend toward compression of the rachis occurring in the Glaucidiaceae-Hydrastidaceae line and in some Berberidaceae. 2. Leaves palmately compound in some Lardizabalaceae. 3. Leaves bipinnately compound in Nandinaceae. 4. Leaves basically simple in Menispermaceae (but a few advanced types ternately compound!) and Sabiaceae (excluding Meliosmaceae), both with a distinctive fimbrial vein, and in Circaeasteraceae. 5. Actinodromous venation developing in several lines of Menispermaceae, coupled with extension of the secondary veins to the fimbrial vein.

Order 10. Papaverales

Leaves basically pinnately compound; margin toothed, teeth of specialized types including Spinose; exstipulate; latex present.

Ranunculid Tooth Types

1. *Chloranthoid*—Ch (Figs. 2, 9)—Ranunculaceae, Glaucidiaceae, Hydrastidaceae, Podophyllaceae. Described under the Magnoliidae.

2. *Spinose*—Sp (Fig. 2)—Berberidaceae, Papaveraceae. Medial vein emerging as a spine.

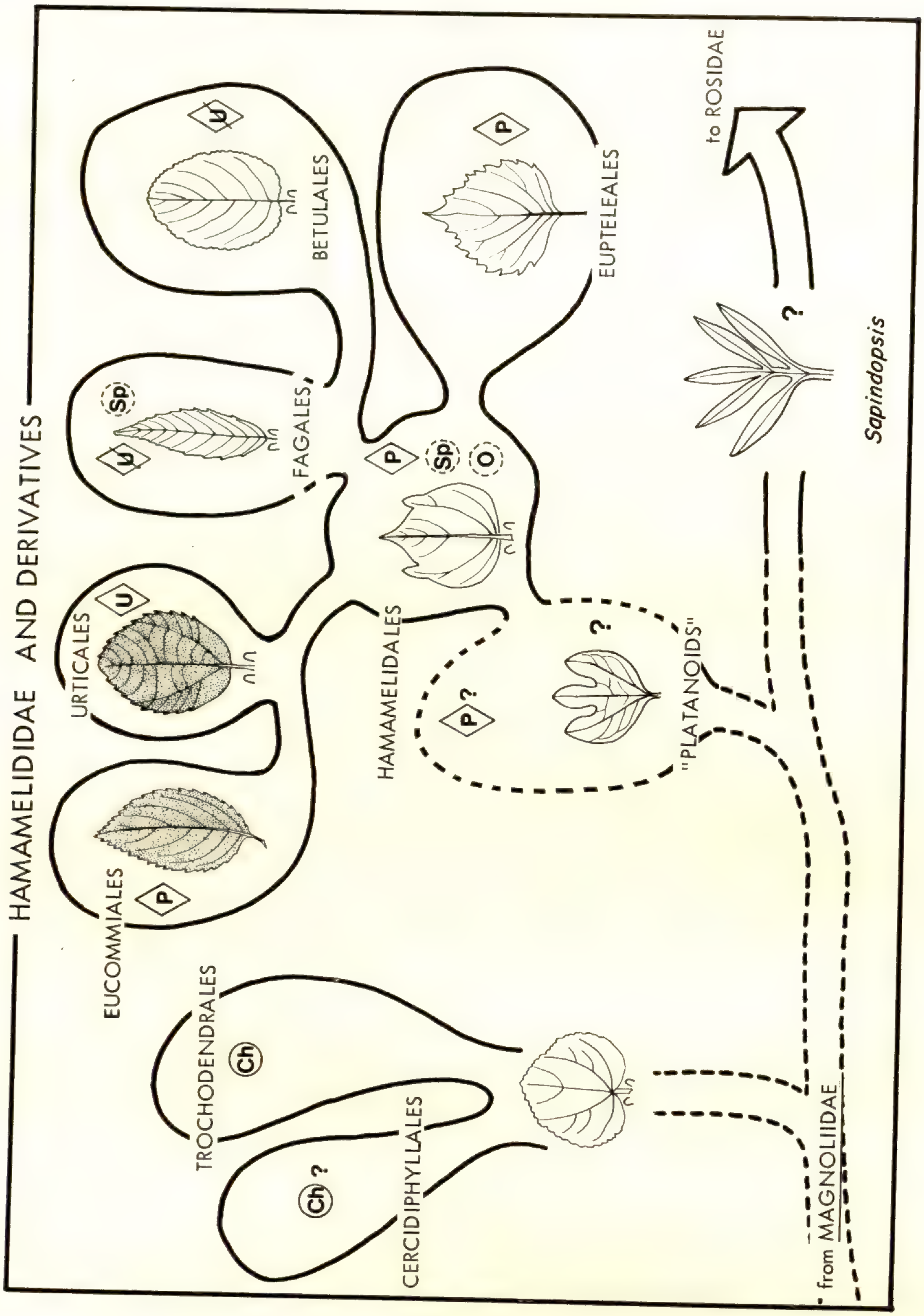
SUBCLASS C. HAMAMELIDIDAE

Leaves simple; margin basically toothed; venation actinodromous; secondary veins brochidodromous; tertiary venation transverse; glands lacking; stipulate (Fig. 10).

Trends: 1. Unlobed palmately veined leaves with incurving primaries in the Trochodendrales, Cercidiphyllales, and some of the Hamamelidales. 2. Palmately lobed leaves in the Platanaceae and Hamamelidaceae. 3. Pinnate venation by suppression of the lateral primaries in Trochodendraceae, some Hamamelidaceae, some Urticales, Fagales, and Myricales. Basally congested secondary veins occurring in these orders are inferred to result from this suppression. 4. Tertiary venation becoming closely spaced and rigidly transverse in the more advanced orders.

Order 12. Trochodendrales

Leaves simple; margin with Chloranthoid Teeth; venation actinodromous; intercostal venation transverse; glands lacking; stipulate.


to ROSIDAE
BETULALES
EUPTELEALES
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URTICALES
EUCOMMIALES
HAMAMELIDALES
"PLATANOIDS"
TROCHODENDRALES
CERCIDIPHYLLALES
Sapindopsis
from MAGNOLIIDAE
HAMAMELIDIDAE AND D

Trend: Becoming exstipulate and pinnately veined in Trochodendraceae but with the secondary veins congested toward the leaf base.

Order 13. Cercidiphyllales

Leaves simple; margin with convex-convex crenations having a medial vein terminating at the apex and with converging higher order lateral veins (Fig. 11). These teeth possibly represent modified Chloranthoid Teeth. Primary venation inwardly curving actinodromous; secondary veins brochidodromous; stipulate.

Both this and the preceding order with their unlobed leaves and Chloranthoid Teeth possibly derive from a different ancestor than the other Hamamelididae and may not be directly related to lines having had their origins in the lobate "Platanoid" stage (see Fig. 10 and Hamamelidales, below).

Order 14. Eupteleales

Leaves simple; margin with Platanoid Teeth (Figs. 2, 11); venation pinnate; secondary veins craspedodromous and congested toward the leaf base, possibly indicating an actinodromous origin; tertiary venation transverse; exstipulate.

Order 15. Didymelales

To the Dilleniidae; cf. Wolfe (1973).

Order 16. Hamamelidales

Leaves simple, palmately lobed; margin with Platanoid Teeth; venation actinodromous; secondary veins brochidodromous; intercostal venation transverse; stipulate.

Trends: 1. A line of middle and Late Cretaceous leaves termed the "Platanoids" are tentatively regarded as possible early members of the trend toward the hamamelid line (Doyle & Hickey, in press). These are simple palmately lobed leaves with entire margins, palinactinodromous primary veins, and intercostal venation which shows an increase in regularity from random to rigidly percurrent in progressively younger occurrences (Fig. 10). 2. In the fossil record of the Late Cretaceous and Early Tertiary a highly diverse group of probable hamamelids occurred including palmately lobed leaves (*Pseudoaspidophyllum*), secondarily simple and peltate types (*Protophyllum*), and a palmately trifoliolately compound type (*"Cissus" marginata*). The modern family Platanaceae is probably a relict of this radiation. 3. Extreme reduction of the blade in Myrothamnaceae. 4. To specialized non-glandular teeth with convergent higher order lateral veins such as the Spinose type (*Sinowilsonia* and *Corylopsis*) where the medial vein projects beyond the tooth apex; or in *Altingia* where the

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FIGURE 10. Leaf affinities of the Hamamelididae and derivatives. Tooth types believed to have a common ancestry are indicated by the letters within the same symbols, such as the circle or the diamond. Ch = Chloranthoid; P = Platanoid; U and Ⱶ = Urticoid and Modified Urticoid; Sp = Spinose; and O = Other types. Possible affinity to the fossil "Platanoid" group and to *Sapindopsis* of Cretaceous age is indicated by question marks. Latex is indicated by the stippled pattern.

medial vein terminates at the tooth apex which is capped by a glandular nipple (i.e., papilla). 5. Numerous entire-margined forms such as *Disanthus*. 6. Primary veins approaching acrodromy (*Disanthus*). 7. Venation becoming pinnate by suppression of the basal primary veins (*Corylopsis, Hamamelis, Fothergillia*). The early Late Cretaceous form *Betulites* is a possible representative of this group as well.

Order 17. Eucommiales

Leaves simple; margin with glandular Platanoid Teeth; venation pinnate; secondary veins camptodromous; tertiary venation transverse; exstipulate; latex present.

Order 18. Urticales

Leaves simple; margin with non-glandular Urticoid Teeth; venation palmate; secondary veins craspedodromous; tertiary venation strongly transverse; stipulate, latex present.

Trends: 1. To palmately compound in Cannabaceae. 2. Venation trending from actinodromous to acrodromous in many Urticaceae and some Ulmaceae. 3. Venation becoming pinnate in many Ulmaceae and Moraceae. Ulmaceae also show a trend from pinnate leaves with symmetrical bases in *Chaetoptelea* to an asymmetrical base in *Ulmus*. 4. Characteristic composite intersecondary veins develop in the Moraceae by strengthening of the anastomoses of the alternate percurrent tertiary veins in the middle of the intercostal area.

Order 21. Fagales

Leaves simple; margin with non-glandular teeth having their midvein terminating at or somewhat beyond the apex (a modified Urticoid Tooth ? or possibly a Cunonioid Tooth in *Trigonobalanus* ?) or with Spinose Teeth; venation pinnate; tertiary venation strongly transverse; stipulate. Leaf affinities uncertain.

Order 22. Betulales

Leaves simple; margin with non-glandular, possibly modified Urticoid Teeth; venation pinnate although the basal pair of secondaries is possibly homologous to the lateral primaries; secondary veins craspedodromous; tertiary venation strongly transverse; stipulate.

Order 23. Balanopales

Leaves simple; margin entire; venation pinnate; secondary veins irregular camptodromous; tertiary venation random; exstipulate.

Order 24. Myricales

Leaves simple; margin toothed; venation pinnate; secondary veins semicraspedodromous; laminar glands present; stipulate. The leaves of this and the preceding order provide no systematically important characters; thus Takhtajan's assignment is retained.

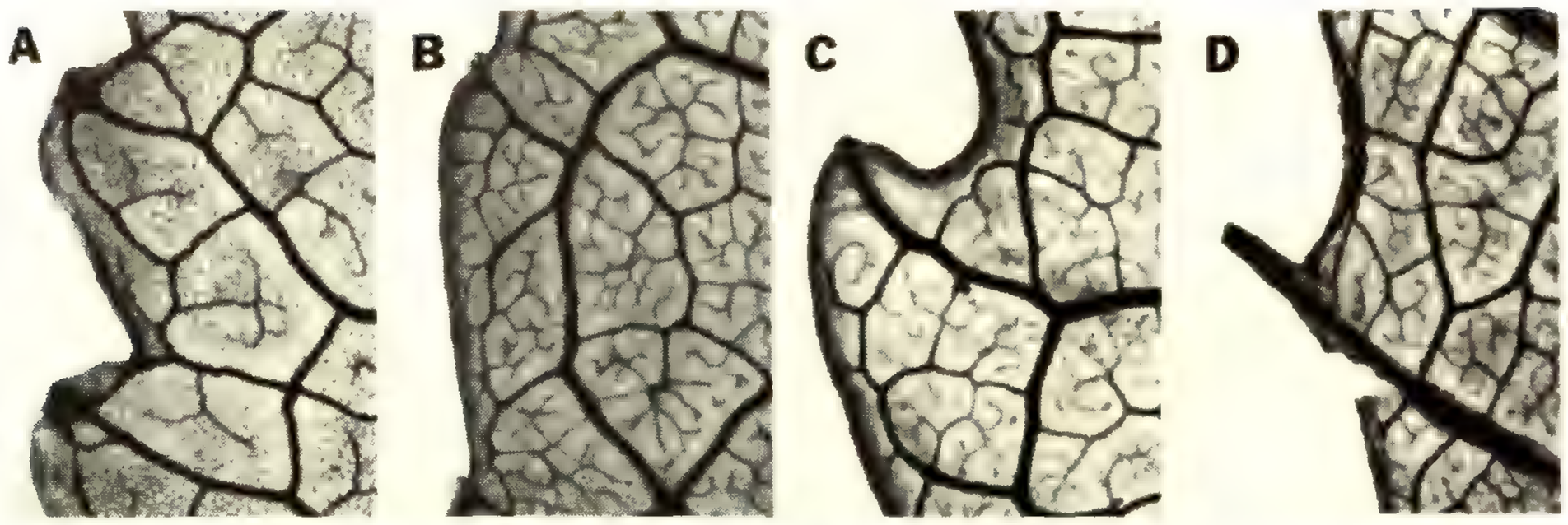

FIGURE 11. Tooth types of the Hamamelididae; all × 10.—A. Chloranthoid; *Tetracentron sinense* Oliv. (Tetracentraceae); China: Hupeh, *Wilson 2156* (US).—B. *Cercidiphyllum japonicum* Sieb. & Zucc. (Cercidiphyllaceae); Japan: Nikko, *Collector Unknown* (US 1314866).—C. *Altingia excelsa* Noronka (Hamamelidaceae); China: Yunnan, *Rock 7174* (US).—D. *Corylopsis glabrescens* Franch. & Sav. (Hamamelidaceae); USA: Pennsylvania, *Walker 7663* (US).

Order 25. Juglandales

To the subclass Rosidae; cf. Wolfe (1973).

Order 26. Leitneriales

Leaves simple; margin entire; venation pinnate; secondary veins camptodromous; tertiary venation strongly transverse.

Hamamelid Tooth Types

1. *Chloranthoid*—Ch (Figs. 2, 11)—Trochodendrales and possibly in a modified form in the Cercidiphyllales. Described under the Magnoliidae.

2. *Platanoid*—P (Figs. 2, 11)—Eupteleales, some Hamamelidales (*Platanus*, some Hamamelidaceae), Eucommiales. Teeth with a medial secondary vein becoming attenuated toward a glandular apex where it opens into a cavity or foramen; medial vein accompanied by higher order laterals forming a series of brochidodromous loops with the upper pair converging on, but not reaching, the medial vein.

3. *Urticoid*—U (Figs. 2, 11)—Urticales. A non-glandular tooth having a medial secondary vein terminating at or near its apex with convergent higher order lateral veins. A somewhat modified form (Ⱆ) which is shorter and broader than the typical Urticoid Type is found in the Fagales and the Betulales.

4. Various other types—either highly specialized or derived:
   a. *Spinose*—Sp (Fig. 2)—Hamamelidaceae (*Sinowilsonia, Corylopsis*), and some Fagales. Medial vein projecting beyond the tooth apex; non-glandular, possibly derived from the Platanoid or Urticoid types by recession of the margin.
   b. *Fothergillia Type—Fothergillia.* Medial secondary terminating at the base of a clear glandular apical nipple or papilla; convergent higher order lateral veins present; tooth possibly derived from the Platanoid Type.

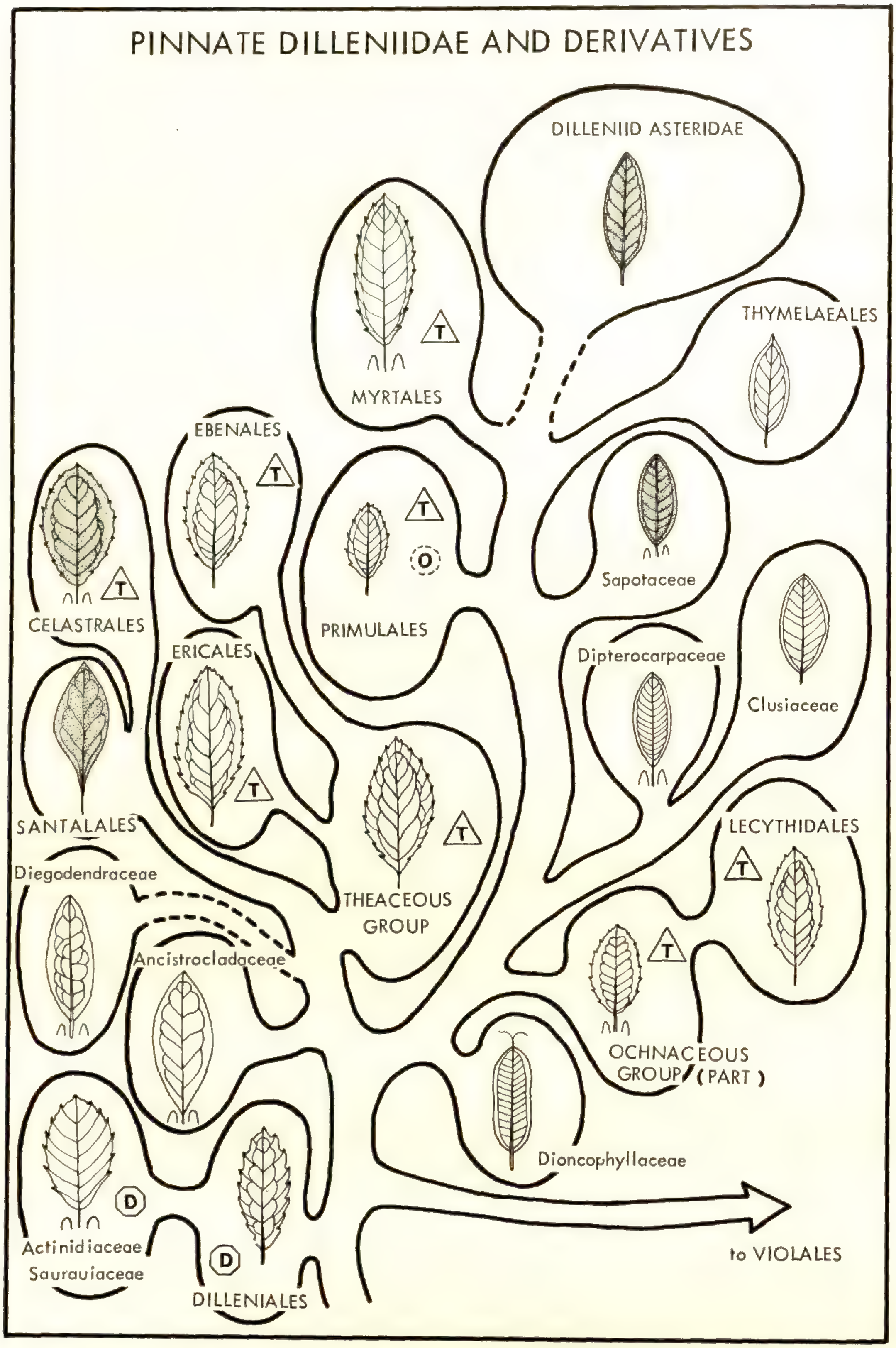

FIGURE 12. Leaf affinities in the Pinnate Dilleniidae and derivatives. Separation into a Theaceous Group on the left and an Ochnaceous Group on the right is shown in the diagram.

SUBCLASS D. CARYOPHYLLIDAE

Leaves simple; margin entire; venation pinnate; secondary veins irregularly brochidodromous; tertiary venation poorly developed, random and not transverse; leaves thick and fleshy or mealy, staining poorly in Safranin O; stipulate (Fig. 7).

Trends: 1. Strengthening of the basal pair of secondaries into primaries with the development of incipient basal lobes, giving rise to a tri-nerved, halberd-shaped leaf. 2. Many xerophytic and halophytic reductions especially toward oblong, entire-margined leaves with tri-nerved, imperfect acrodromous venation. 3. In secondarily woody, arborescent forms such as *Coccoloba* and *Charpentiera* the intercostal venation becomes transversely oriented. 4. Fusion of separate stipules into the basal sheath.

The orders of the Caryophyllidae are not analyzed in this survey.

SUBCLASS E. DILLENIIDAE

Leaves basically simple; margin toothed; venation pinnate; secondary veins semicraspedodromous; tertiary venation random with a tendency toward admedial orientation; glands present on teeth; stipulate (Figs. 12–13).

Trends: 1. Development of pinnately compound leaves in the Crossosomataceae and Quiinaceae. 2. Glandular teeth modified in a number of ways, especially in the Palmate Dilleniids, or lost. 3. Development of the Theoid Tooth in the ancestor of the Theaceous and Ochnaceous Alliances of the Pinnate Dilleniids and of the Palmate Dilleniids and further modifications of this type. 4. Development of actinodromous venation (leading to campylodromous) in the Palmate Dilleniids. 5. Development of a strongly transverse tertiary venation in the Dilleniales, the Actinidiaceous Group, and in the Palmate Dilleniids. 6. Development of tertiary venation paralleling the secondary veins in the Ochnaceous Alliance of the Pinnate Dilleniids. 7. Development of an intramarginal vein in the Ochnaceous Alliance and in the Primulales and the Myrtales. 8. Loss of stipules in many of the higher Dilleniidae as well as in scattered families. 9. Becoming laticiferous in numerous lines.

I. Pinnate Dilleniidae

Leaves basically simple; margin with glandular teeth; venation pinnate; secondary veins semicraspedodromous; tertiary venation random with a tendency toward admedial orientation; stipulate (Fig. 12).

Trends: 1. Development of the glandular setaceous Theoid Tooth in the forerunner of all but the Dilleniales and their inferred derivatives the Actinidiaceous Group (Figs. 3, 15). 2. Development of the Dillenioid Tooth with a clear glandular or expanded apex in the Dilleniales, or its retention there as a primitive

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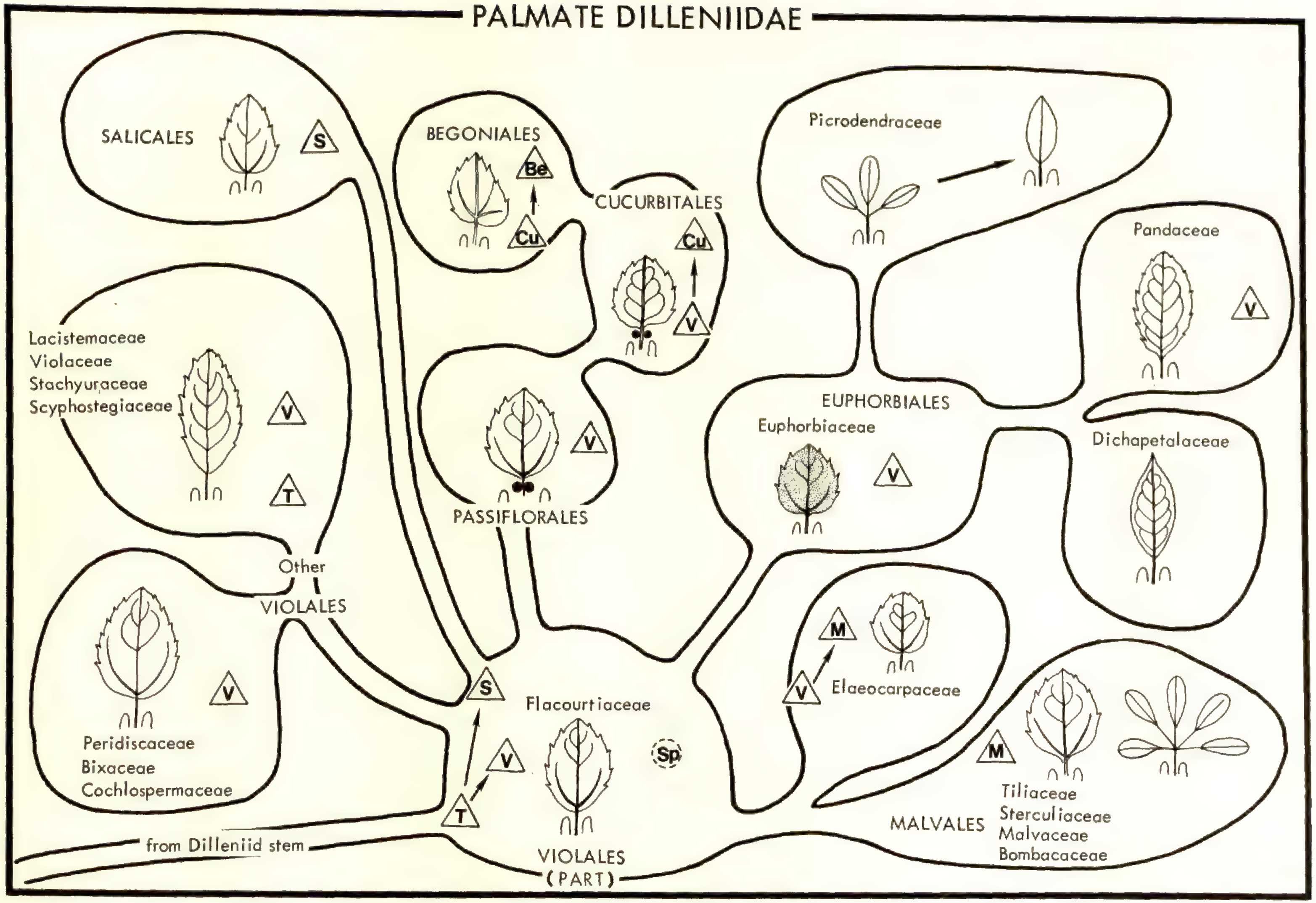
Note also the inferred derivation of the Dilleniid-Leafed Asteridae from the Ochnaceous Group. Dillenioid Tooth type is indicated by the letter D in the hexagon, the Theoid Tooth by the T in the triangle, and other types by the letter O within the dashed circle. Latex is indicated by the stippled pattern.


PALMATE DILLENIIDAE
SALICALES
S
BEGONIALES
Be
Cu
CUCURBITALES
Cu
V
Picrodendraceae
Pandaceae
V
Lacistemaceae
Violaceae
Stachyuraceae
Scyphostegiaceae
V
T
V
PASSIFLORALES
EUPHORBIALES
Euphorbiaceae
V
Dichapetalaceae
Other
VIOLALES
M
V
Elaeocarpaceae
V
Peridiscaceae
Bixaceae
Cochlospermaceae
S
Flacourtiaceae
V
T
Sp
M
Tiliaceae
Sterculiaceae
Malvaceae
Bombacaceae
MALVALES
from Dilleniid stem
VIOLALES
(PART)

feature, and its modification into a Spinose Tooth (Fig. 15). 3. Often with highly characteristic apical prolongation of the secondary loops in the Theaceous Alliance (Fig. 14). 4. Development of an intramarginal vein in the Ochnaceous Alliance. 5. Development of strongly percurrent tertiary venation in the Dilleniaceae, Actinidiaceae, and Saurauiaceae. 6. Development of weakly transverse intercostal venation in the Theaceous Group and of intercostal venation paralleling the secondaries in the Ochnaceous Group.

Order 31. Dilleniales

Leaves simple; margin with Dillenioid Teeth having a clear glandular or expanded apex; venation pinnate; secondary veins probably basically semicraspedodromous; intercostal venation random; stipulate.

Trends: 1. Development of an intramarginal vein (*Hibbertia*) (Fig. 6). 2. Development of craspedodromous secondary venation. 3. Development of rigidly percurrent tertiary venation in all genera of the Dilleniaceae except *Hibbertia*.

Leaves of this order, as presently constituted, do not include enough generalized characters to be regarded as ancestral to those of the remaining Dilleniids. Only *Hibbertia* has a generalized venation pattern, but most of the toothed forms of this genus have a clear glandular vein termination. However, teeth of the Australian species *Hibbertia dentata*, which have clear glandular deciduous tips, possibly represent the survival of a tooth type which later became the opaque glandular setaceous Theoid type which appears to be basic for all of the remaining Dilleniids except the Actinidiaceous Group.

31a. Actinidiaceous Group (including the Saurauiaceae)

Apparently derived directly from the Dilleniales. Leaves simple, margin with Dillenioid Teeth; venation pinnate; secondary veins craspedodromous; tertiary venation rigidly percurrent; stipulate.

A. Theaceous Alliance

A morphological grouping of those Pinnate Dilleniid leaves having margins with Theoid Teeth; secondary veins basically brochidodromous often forming highly ascending arches (Fig. 14); tertiary venation tending to become at least weakly transverse rather than parallel to the secondaries as in the Ochnaceous Alliance; exstipulate.

33. Theaceous Group (Takhtajan's Order 33, Theales, in part, consisting of Theaceae, Marcgraviaceae, Pentaphylacaceae, Tetrameristaceae, Caryocaraceae, Asteropeiaceae, Pellicieraceae, Bonnetiaceae)

Leaves simple; margin with Theoid Teeth; venation pinnate; secondary veins

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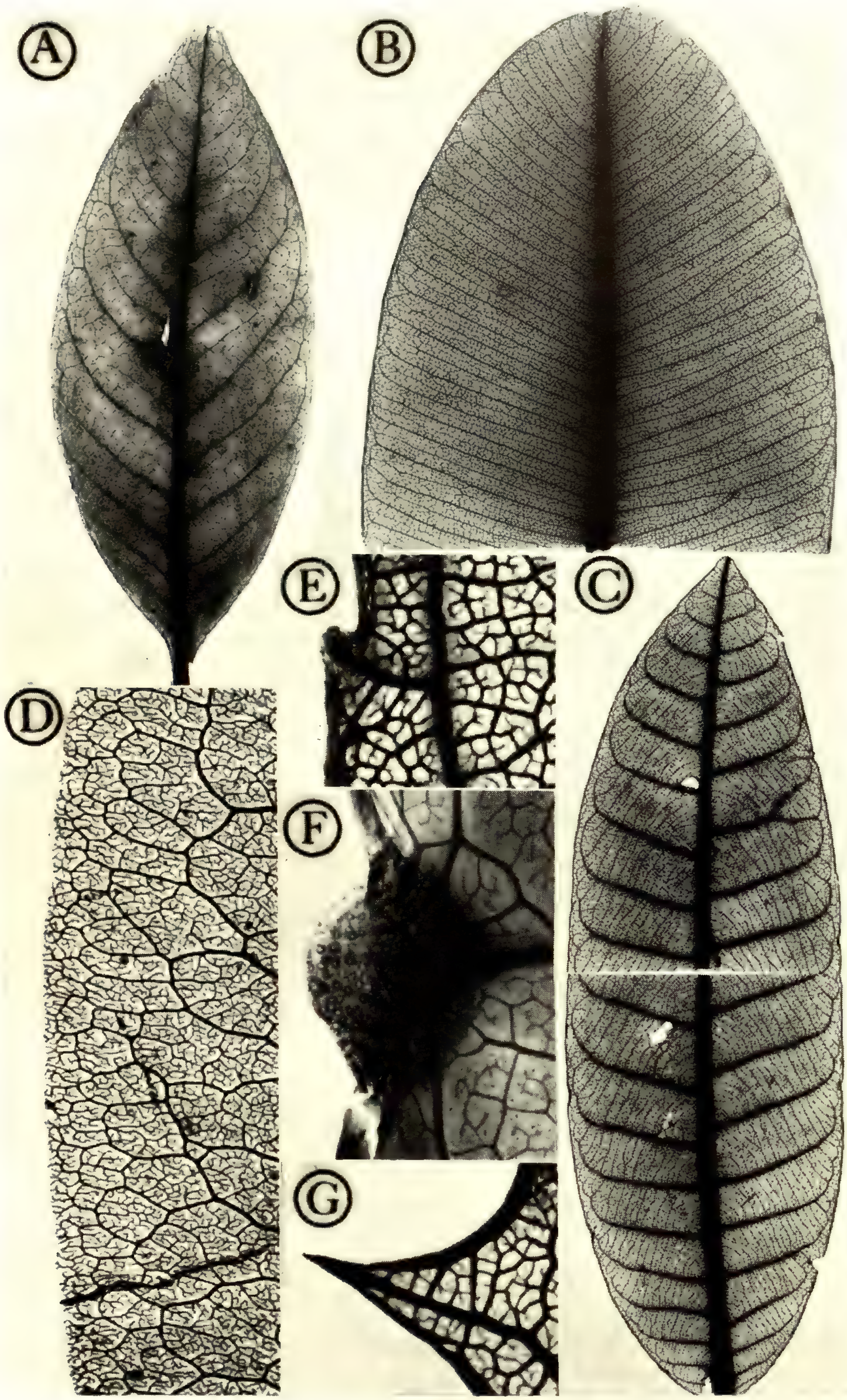
FIGURE 13. Leaf affinities of the Palmate Dilleniidae. Derivatives of the Theoid Tooth are indicated by the letter in the triangular symbol. T = Theoid Tooth, V = Violoid Tooth, S = Salicoid Tooth, Cu = Cucurbitoid Tooth, Be = Begonioid Tooth, M = Malvoid Tooth, Sp = Spinose Tooth. Presence of latex is indicated by the stippled pattern. Acropetiolar glands indicated by the dark circles on the petioles of the Passiflorales and Cucurbitales.


A
B
E
C
D
F
G

brochidodromous often with ascending arches; tertiary venation random to weakly percurrent; basically exstipulate.

Trends: 1. Loss of marginal teeth followed by loss of marginal glands due to marginal enrollment during ontogeny. 2. Increase in transverse tertiary vein orientation. 3. Rarely becoming laticiferous as in *Ficalhoa* (Theaceae).

Order 41. Ericales (excluding the Saurauiaceae and the Actinidiaceae)

Leaves simple; margin with Theoid Teeth; venation pinnate, secondary veins ascending brochidodromous; tertiary venation only weakly transverse; exstipulate.

Trends: 1. Loss of marginal teeth through marginal enrollment during ontogeny. 2. Increasing randomization of the intercostal venation.

In both the Ericales and the Ebenales the weakly transverse intercostal venation tends to be compensated for by the distal branching of the secondaries into a reticulodromous pattern. These secondary branches are then joined to brace the leaf margin (Fig. 14).

Order 42. Diapensiales

Not analyzed.

Order 43. Ebenales (excluding the Sapotaceae)

Leaves simple; margin with Theoid Teeth; venation pinnate; secondary veins eucamptodromous to ascending brochidodromous to reticulodromous with the margin frequently braced by the anastomosing distal branches of the secondaries; tertiary venation ramified to irregularly transverse; exstipulate; latex absent.

Trends: 1. Loss of marginal teeth. 2. Tertiaries becoming moderately percurrent (*Diospyros*).

Order 61. Celastrales

Leaves simple; margin with Theoid Teeth; venation pinnate; secondary veins brochidodromous with apically elongated arches; tertiary veins weakly transverse; stipulate; latex present.

Trends: 1. To entire margins. 2. Eucamptodromous secondary venation. 3. Craspedodromous secondaries in some Aquifoliaceae. 4. Veinlets with numerous branches in Icacinaceae.

In the Takhtajan and Cronquist systems this order is allied to the Rosidae although it shows no trace of a compound-leafed ancestry (Cronquist, 1968:

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FIGURE 14. Some features of leaves of Dilleniidae.—A. Apical prolongation of brochidodromous arches; *Schima confertifolia* Merr. (Theaceae); China: Kwangtung, *Levine 1346* (US); × 1.—B–C. Patterns of ochnalean venation.—B. *Kielmeyera coriacea* Mart. (Clusiaceae); Brazil: *Irwin et al. 10870* (US); × 1.—C. *Caraipa punctatula* Ducke (Clusiaceae); Brazil: *Ducke 35410* (US); × 1.—D. Ericaceous reticulodromous marginal venation; *Befaria glauca* Humb. & Bonpl. (Ericaceae); Colombia: *Cuatrecasas 13384* (US); × 5.—E–G. Some inferred variants of the Theoid Tooth; all × 10.—E. Violoid; *Banara domingensis* Benth. (Flacourtiaceae); Dominican Republic: *Ekman 10898* (US).—F. Cucurbitoid; *Fevillea cordifolia* L. (Cucurbitaceae); Peru: *Woytkowski 7607* (US).—G. Spinose; *Casearia crassinervis* Urb. (Flacourtiaceae); Cuba: Oriente Province, *León & Allain 19331* (US).

255), a character we believe is basic to that subclass. In addition, two families of the Celastrales, the Aquifoliaceae and the Celastraceae, have Theoid Teeth with deciduous seta. In most of the Celastrales these teeth are strongly modified or the apex is turned inward close to the sinus, but typical Theoid Teeth occur in the two U.S. National Herbarium specimens identified as *Celastrus novo-guinensis* Merr. and Perry (Eastern New Guinea: Mt. Wilhelm, E slope, 6 July 1959, 2770 m, *Brass 30337*; Arau, 21 October 1959, 1400 m, *Brass 32222*). In addition, leaves of the Celastrales show the same apically elongate secondary arches and generally weakly transverse tertiary venation as in the Theaceous Alliance of the Dilleniidae.

Placement of this order with centripetal stamen maturation in the Dilleniidae would indicate that this feature—rather than being a fundamental determinate of Rosid affinity, as in Cronquist's system—may have had an independent origin within the dilleniid line (see discussion in Philipson, 1974). Hutchinson (1973) also places the Celastrales within the context of the Dilleniidae when he derives it from either the Theales or the Tiliaceae.

Order 64. Santalales

Leaves simple, base tending to be decurrent into the petiole; margin entire (if the disputed Dipentodontaceae and Medusandraceae—both toothed—are excluded); venation basically pinnate; secondary veins irregularly brochidodromous in ascending arches, the basal pair decurrent into the top of the petiole; tertiary venation weakly and distantly transverse; veinlets highly branched; exstipulate; latex present. This basic leaf has many similarities with the exstipulate family Icacinaceae, to which Santalales are reported to be closely related by Takhtajan and Cronquist.

Trends: 1. Reduction of leaves to scales or their complete loss in some genera of the Loranthaceae, and in Cynomoriaceae and Balanophoraceae. 2. To decrease the angle of divergence of the basal secondaries, strengthen these veins (e.g., some Loranthaceae), and to develop acrodromous and actinodromous forms through the process of augmenting these basal secondaries (some Santalaceae, Loranthaceae, Cardiopteridaceae). 3. To eucamptodromy. 4. Reorientation of the tertiaries obliquely across the intercostal area either perpendicular or oblique to the midvein.

Order 5. Rafflesiales

Leaves, when present, reduced to scales, simple; margin entire; veins reduced to two orders, parallelodromous and dichotomously branched, with disjunct distal portions (Sreemadhaven & Hickey, in preparation); petiole lacking.

Leaf evidence for the assignment of this order is insufficient. We simply follow Cronquist here in relating it to the Santalales where superficially similar leaves occur in the more reduced parasitic forms.

B. Ochnaceous Alliance

A morphological grouping of those Pinnate Dilleniids with Theoid Teeth, secondary veins strongly brochidodromous, sometimes in ascending arches but

mostly tending to form an intramarginal vein; tertiary venation obliquely percurrent, tending to become oriented perpendicular to the midvein and eventually parallel to the secondaries (Fig. 12).

Trends: 1. Increased strengthening and straightening of the brochidodromous arch to form an intramarginal vein, accompanied by closer spacing of the secondaries, development of an intersecondary vein paralleling the secondaries, and reorientation of the tertiary system in the same direction (Fig. 14). 2. Loss of stipules. 3. Loss of marginal teeth. 4. Becoming laticiferous in certain lines.

33. Ochnaceous Group (Takhtajan's Order 33, Theales, in part, consisting of Ochnaceae, Lophiraceae, Dipterocarpaceae, Strasburgeriaceae, Ancistrocladaceae, Dioncophyllaceae, Diegodendraceae, Quiinaceae, Medusagynaceae, Oncothecaceae, Clusiaceae, Hypericaceae, and Elatinaceae)

Leaves simple; margin with Theoid Teeth; venation pinnate; secondary veins strongly brochidodromous often forming an intramarginal vein by strengthening and straightening of the outer portion of the arc, more rarely ascending brochidodromous or eucamptodromous; secondaries tending to become closely spaced in the strongly brochidodromous forms; intercostal areas with a medial intersecondary vein to the arch; tertiary venation obliquely percurrent, tending to become oriented perpendicular to the midvein and eventually parallel to the secondaries; stipulate (Fig. 14).

Trends: 1. To pinnately compound leaves in the Quiinaceae. 2. Formation of an intramarginal vein by strengthening and straightening of the brochidodromous secondary arches. Development of this vein as the principal barrier to tearing from the margin appears to be accompanied by withdrawal of the margin to a position just outside the intramarginal vein. Marginal teeth and glands are also progressively lost during this process and the tertiary intercostal veins often become oriented parallel to the secondaries. We infer that marginal withdrawal and loss of teeth is due to premature cessation of marginal growth and that the parallel orientation of the tertiary veins becomes possible where they are not needed as reinforcements against ripping from the margin. 3. Secondary redevelopment of apparently transverse tertiary veins by the strengthening and fusion of the quaternary vein segments connecting admedially orientated tertiaries with the concomitant reduction in strength of the tertiaries (Dipterocarpaceae).

Order 33b. Lecythidales (Lecythidaceae in the broad sense including the Asteranthaceae, Barringtoniaceae, Foetidiaceae, and Napoleonaceae)

Leaves basically simple; margin with Theoid Teeth; venation pinnate; secondary veins brochidodromous; tertiary venation admedially ramified to weakly transverse; exstipulate.

Family 155. Sapotaceae

Leaves simple; margin entire; venation pinnate; secondary veins irregularly brochidodromous to eucamptodromous; tertiary venation obliquely and irregularly percurrent, tending to be oriented perpendicular to the midvein; stipulate; latex present.

Trends: 1. Brochidodromous arch becoming straighter and more regular, forming an intramarginal vein in the Mimusopeae and in other genera such as *Butyrospermum* and *Planchonella.* 2. Secondaries becoming closely spaced in brochidodromous forms and a medial intersecondary vein developing (*Chrysophyllum*). 3. Tertiaries oriented parallel to the secondaries in the Mimusopeae.

This family with its latex system, trilacunar nodes, unitegmic ovules, pubescence of two-armed hairs, and ochnalean venation is anomalous within the Ebenales, which are without latex, unilacunar, often bitegmic, lacking in two-armed hairs, and have leaves of the thealean venation pattern.

Order 44. Primulales

Leaves simple; margin with Theoid Teeth (in Theophrastaceae only); secondary veins brochidodromous to eucamptodromous; tertiary venation irregularly transverse; exstipulate; latex absent.

Trends: 1. Loss of marginal teeth in most genera. Modified teeth are retained in *Maesa* (Myrsinaceae) where they are coarse, doubly concave, and have a glandular swelling at the end of a medial vein branch which frequently recurves upon entering the tooth. Primulaceae retain a swollen non-deciduous glandular cap. 2. Development of acrodromous leaves in *Jacquinia* possibly by strengthening of the double brochidodromous arches (an inner and an outer) characteristic of the Theophrastaceae. 3. Development of an intramarginal vein. 4. Orientation of tertiaries perpendicular to the midvein and in strongly brochidodromous forms these often become oriented parallel to the secondaries.

Order 47. Thymelaeales (including Didymelaceae)

Leaves simple; margin entire; venation pinnate; secondary veins brochidodromous and forming an intramarginal vein with the secondaries forking conspicuously as they join it; tertiary venation random to weakly transverse; glands lacking; exstipulate.

Trends: 1. Loss of intramarginal vein; secondaries become eucamptodromous. 2. Increasing irregularity of secondaries.

Order 54. Myrtales

Leaves simple; margin basically entire, but primitively with Theoid Teeth (Rhizophoraceae); venation pinnate; secondary veins brochidodromous; tertiary venation obliquely and irregularly percurrent; stipulate; latex absent.

Trends: 1. Development of intramarginal veins in most families, especially in the Myrtaceae. This is accompanied by reorientation of the transverse tertiary network parallel to the secondaries and development of a medial intersecondary vein. 2. Development of acrodromous venation apparently by strengthening of the outer intramarginal vein and the next highest secondary vein which forms an inner brochidodromous arch. Our model then postulates the broadening of these acrodromous secondaries into primaries and the migration of the upper pair to a basal position. Inferred transitions from brochidodromous with a weak intramarginal vein through suprabasal to basal acrodromous can be seen in the Memecylaceae into the Melastomataceae and independently in the Anisophyl-

leaceae. 3. Development of eucamptodromous secondaries in the Combretaceae. 4. Loss of stipules.

Despite the absence of internal phloem in Rhizophoraceae, the leaf architecture of this family coincides closely with that of the Myrtalean families to which Takhtajan assigns it and not at all to the Cornales where Cronquist places it. We have thus treated its leaf architecture with the Myrtales.

Description of the leaf architecture of the Myrtales with the Dilleniidae presents another important case where leaf morphology yields evidence which runs counter to the assignment of an order to the Rosidae on the basis of other organs. In this case the ochnalean venation pattern, presence of Theoid Teeth, and the apparent lack of compound-leaf ancestors influence us to treat its leaf architecture with the Dilleniidae. On the other hand, the centripetal stamen maturation direction and the pollen of most of the Myrtales, except the Rhizophoraceae, indicate Rosid affinities (Doyle, personal communication). If the Rhizophoraceae is excluded from the order, then the Theoid Tooth is not part of Myrtalean leaf architecture, and the Myrtales possibly represent a trend in the Rosids paralleling the Ochnalean Group in developing strongly brochidodromous secondaries and intramarginal veins and in having modifications of the tertiary venation similar to the ochnalean pattern. More evidence, especially from carefully studied fossil leaves and comparative morphology, will be needed to resolve this seeming contradiction.

II. Palmate Dilleniidae

Leaves basically simple; margin with glandular teeth; venation actinodromous; secondary veins semicraspedodromous; tertiary venation weakly transverse; stipulate (Fig. 13).

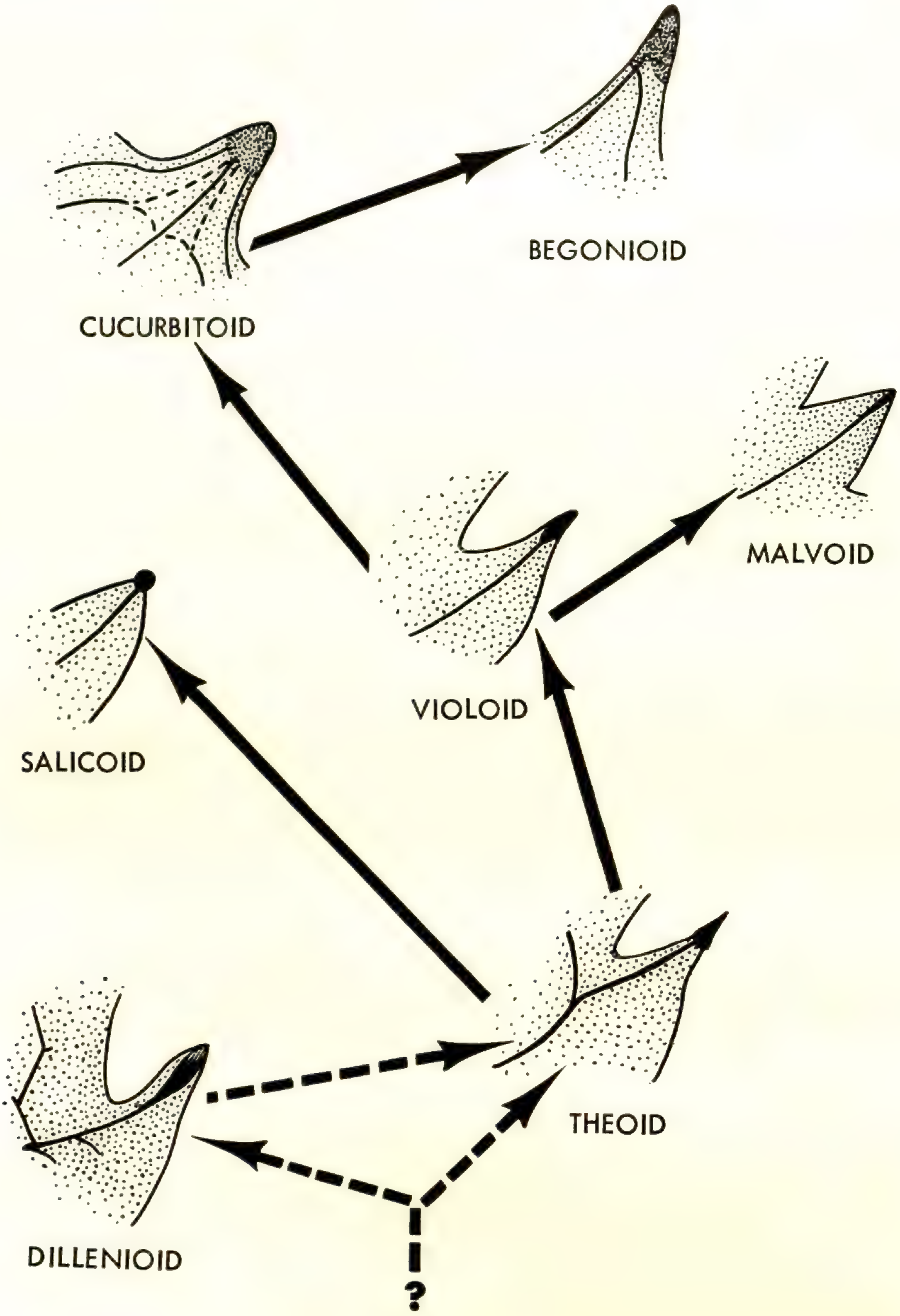
Trends: 1. Leaves becoming palmately compound in some Passiflorales, Malvales, and Euphorbiales. 2. Modification of the primitive Theoid Tooth by fusion of the glandular seta to the tooth apex in the Violales, Passiflorales, Malvales, and Euphorbiales; by loss of glandular function in the Malvales; or by other specialized modifications in the Violales, Salicales, Cucurbitales, and Begoniales (Fig. 15). 3. Development of pinnate venation by weakening of the lateral primaries in all orders but Begoniales. 4. Development of strongly transverse tertiary venation which is characteristically oriented in a concentric fashion in relation to the leaf base. 5. Becoming laticiferous in the Euphorbiales.

Order 34. Violales

Leaves simple; margin with Theoid Teeth; venation imperfectly or incipiently actinodromous; secondary veins semicraspedodromous; tertiary venation weakly transverse; stipulate.

Trends: 1. Development of strongly actinodromous or campylodromous leaves in the Peridiscaceae, Bixaceae, Cochlospermaceae, some Violaceae, and many Flacourtiaceae. The primitive tribe Rinoridae of Violaceae has pinnate leaves with the basal secondaries originating from the top of the petiole at a somewhat lower angle than those above, indicating either common origin from the same incipiently actinodromous trend as the Flacourtiaceae (*Berberidopsis*)

DILLENIID TOOTH TYPES AND THEIR PROPOSED PHYLOGENY



or suppression of the lateral primaries. 2. Development of pinnate venation in a number of families by suppression of the lateral primaries. 3. Modification of the Theoid Tooth (Fig. 2) found in many genera of the basal family Flacourtiaceae (including the most primitive *Berberidopsis* and *Carpotroche*) within the family to the: a. Violoid Tooth in flacourtiaceous genera, such as *Xylosma* and *Homalium*, and in the Violaceae, Stachyuraceae, and Cochlospermaceae. b. Salicoid Tooth in the Idesidae of the Flacourtiaceae and thus to the Salicales (Fig. 16). 4. The Theoid Tooth is retained in the Lacistemataceae.

Order 35. Passiflorales

Leaves basically simple; margin with Violoid Teeth; venation actinodromous; acropetiolar nectaries present; stipulate.

Trends: 1. Leaves becoming palmately compound by dissection of lobes. 2. To pinnately veined, simple leaves with basally congested secondary venation. 3. Loss of stipules and nectaries.

Order 36. Cucurbitales

Leaves simple; margin with Violoid Teeth; venation actinodromous; acropetiolar nectaries present; stipulate.

Trends: 1. Development of the Cucurbitoid Tooth from the Violoid Tooth. 2. Development of campylodromous venation. 3. Loss of acropetiolar nectaries.

Order 37. Begoniales

Leaves simple; margin with Cucurbitoid Teeth; venation actinodromous; stipulate; leaf with a pervasive asymmetry of form and venation.

Trends: 1. Development of the Begonioid Tooth in the Begoniaceae. 2. Loss of stipules in the Datiscaceae.

Order 40. Salicales

Leaves simple; margin with Salicoid Teeth inferred to be of common origin with those of *Idesia* in the Flacourtiaceae; venation actinodromous; basilaminar glands present; stipulate.

Trends: 1. Loss of teeth in Arctic species of *Salix*. 2. Venation becoming pinnate in *Salix*.

Order 45. Malvales

Leaves simple; margin with the non-glandular Malvoid Tooth, although primitively with the Violoid Tooth (as in Elaeocarpaceae); venation actinodromous; tertiary venation percurrent, frequently concentrically so; stipulate.

Trends: 1. Palmate dissection of the leaf in Elaeocarpaceae, Tiliaceae, Sterculiaceae, and Bombacaceae. 2. Violoid Tooth becoming the non-glandular Malvoid type in genera of the Elaeocarpaceae, Sterculiaceae, Tiliaceae, and Bombacaceae. 3. Development of both perfect actinodromous and of pinnately veined forms by

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FIGURE 15. Dilleniid tooth types and their proposed phylogeny.

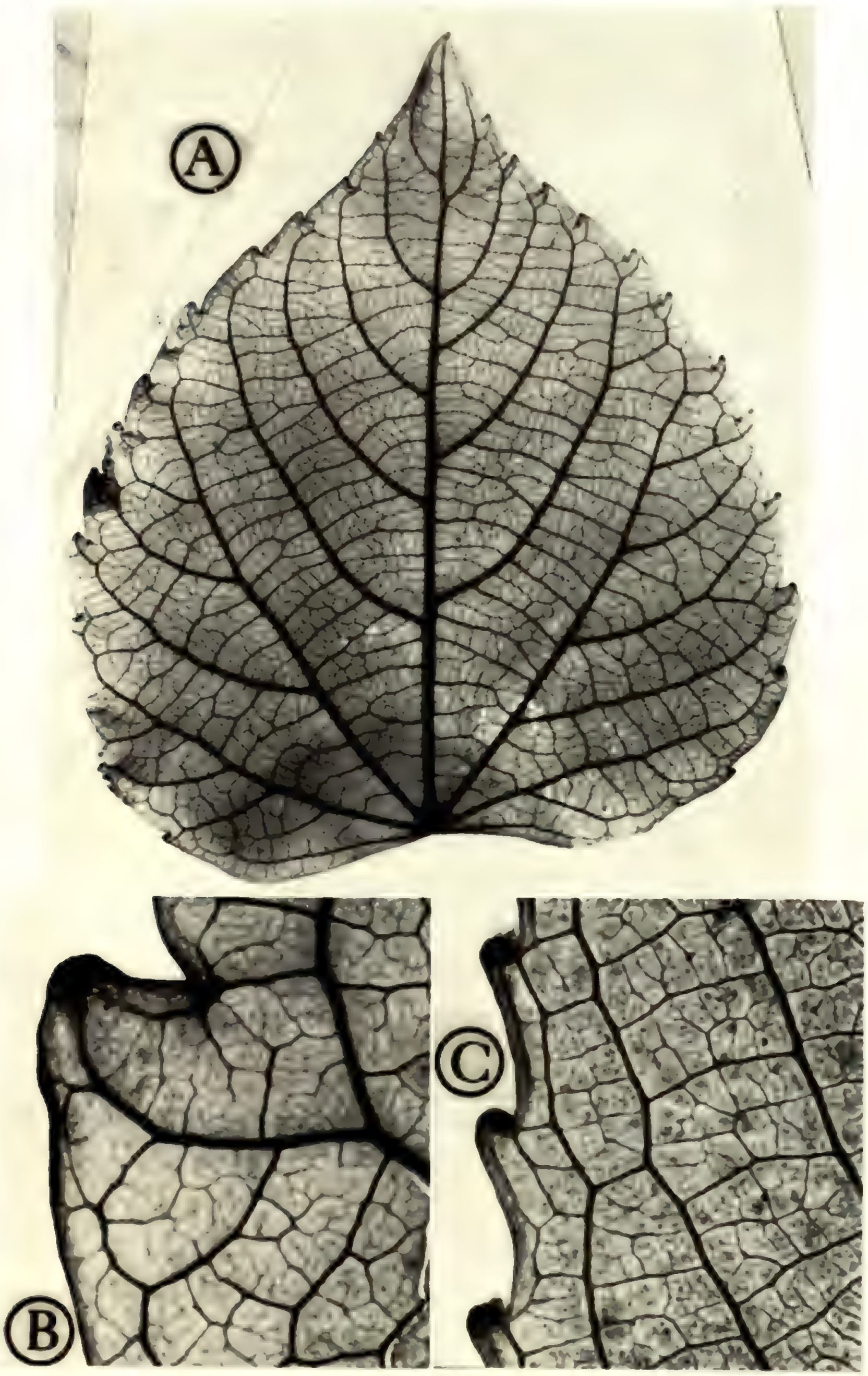
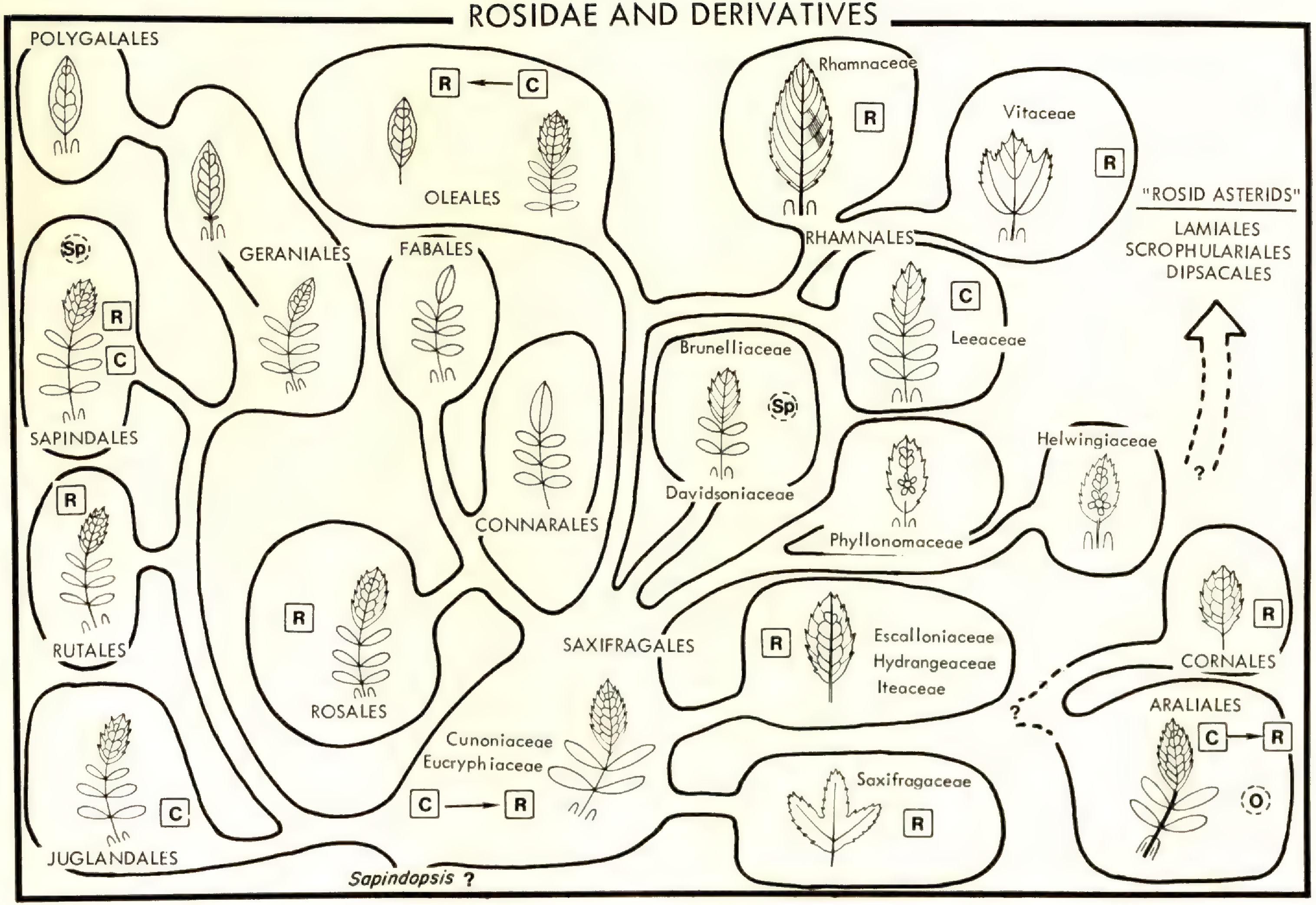


FIGURE 16. Salicoid teeth found in *Idesia polycarpa* Maxim. (Flacourtiaceae); Japan: Nanokawa, *Collector Unknown* (US).—A–B. *Idesia* with the tooth enlarged × 1 and × 10, respectively.—C. Salicoid Tooth in *Salix fragilis* L. (Salicaceae) for comparison; USA: Iowa, *Thorne 13312* (US); × 10.

→

FIGURE 17. Leaf affinities of the Rosidae and derivatives. Possible affinity to the Lower Cretaceous genus *Sapindopsis* is indicated by the question marks. Origin of the Cornales and Araliales is uncertain, as is that of the Rosid Asterids. The symbol on the leaves of Phyllonomaceae and Helwingiaceae represent attached inflorescences. The Cunonioid Tooth and its derivative the Rosoid Tooth are indicated by the letters C and R, respectively, within the squares. Sp within the dashed circle indicates the Spinose Tooth and O in the same symbol indicates a specialized type of tooth of unknown derivation.


ROSIDAE AND DERIVATIVES
POLYGALALES
R
C
OLEALES
Rhamnaceae
R
Vitaceae
R
"ROSID ASTERIDS"
LAMIALES
SCROPHULARIALES
DIPSACALES
GERANIALES
FABALES
RHAMNALES
Sp
R
C
SAPINDALES
Brunelliaceae
Sp
Davidsoniaceae
C
Leeaceae
Helwingiaceae
?
CONNARALES
Phyllonomaceae
R
RUTALES
R
ROSALES
SAXIFRAGALES
R
Escalloniaceae
Hydrangeaceae
Iteaceae
R
CORNALES
?
ARALIALES
C
R
O
Cunoniaceae
Eucryphiaceae
C
R
Saxifragaceae
R
C
JUGLANDALES
Sapindopsis ?

reinforcement or suppression of the lateral primary veins in a possible imperfect actinodromous ancestral form.

Order 46. Euphorbiales

Leaves basically simple; margin with glandular Violoid Teeth; venation imperfect actinodromous; tertiary venation transverse; stipulate; latex present.

Trends: 1. Palmate dissection of the leaf in some Picrodendraceae, Euphorbiaceae, Pandaceae, Dichapetalaceae. 2. Leaf becoming perfect actinodromous. 3. Development of prominent basilaminar and acropetiolar glands.

Principal Dilleniid Tooth Types

1. *Dillenioid*—D (Fig. 15)—Dilleniaceae, Actinidiaceae. Medial vein of the tooth terminating in a clear glandular expanded (papillate) apex, vein often projecting beyond the tooth apex.

2. *Theoid*—T (Figs. 2, 15)—Theaceae, Ochnaceae. Medial vein of the tooth running to the apex, vein end expanded and congested with opaque material. Tooth apex capped by an opaque deciduous seta.

3. *Violoid*—V (Figs. 14–15)—Violaceae, Cochlospermaceae. Medial vein of the tooth running to the apex where it expands into an opaque glandular termination, deciduous apical seta absent.

4. *Salicoid*—S (Figs. 2, 15, 16)—*Idesia*, Salicaceae. An inferred modification of the Theoid Tooth where the seta is retained as a dark, but not opaque, non-deciduous spherical callosity fused to the tooth apex.

5. *Malvoid*—M (Fig. 15)—Malvaceae, Bombacaceae. Medial vein of the tooth running to the apex, non-glandular or apparently so.

6. *Cucurbitoid*—Cu (Figs. 14–15)—Cucurbitaceae, Datiscaceae. Medial vein of the tooth ending in a translucent apical pad of densely packed cells (tylate apex). Lateral veins present and either fusing with the medial vein or connivent with it and terminating in the tylate apex.

7. *Begonioid*—Be (Fig. 15)—Begoniaceae. An inferred asymmetrical modification of the Cucurbitoid Type in which one of the lateral veins appears to be strengthened at the expense of the medial and second lateral.

8. *Spinose*—Sp (Fig. 14)—Flacourtiaceae.

SUBCLASS F. ROSIDAE

Leaves basically pinnately compound; margin with glandular Cunonioid Teeth; venation pinnate; secondary veins semicraspedodromous; tertiary venation transverse; stipulate; latex absent (Fig. 17).

Trends: 1. Development of palmately lobed or palmately compound leaves by inferred shortening of the pinnate rachis in the Saxifragales, Hippuridales, Sapindales, Geraniales, Cornales, and Rhamnales. 2. Development of simple leaves in most orders through reduction to one of the leaflets of pinnate leaves. 3. Origin of the Rosoid Tooth from the Cunonioid Tooth in several lines, apparently independently, as the result of broadening of the tooth (Fig. 18). 4. Origin of the Spinose Tooth from the Cunonioid Tooth in the Sapindales and

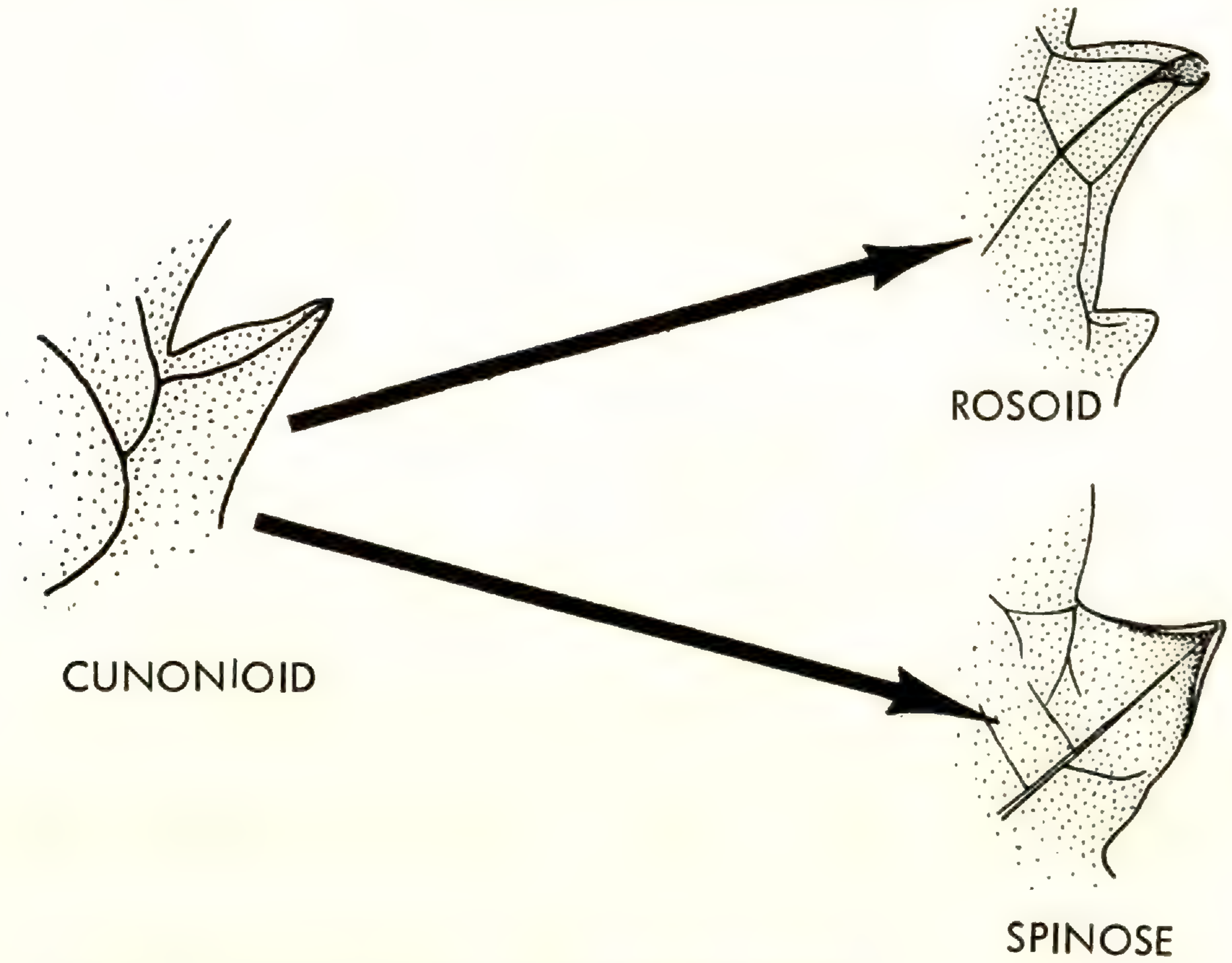


FIGURE 18. Rosid tooth types and their proposed phylogeny.

Saxifragales (Fig. 18). 5. Camptodromous and craspedodromous secondary vein configurations developing from the semicraspedodromous condition. 6. Origin of laminar glands in the superorder Rutanae.

A complex of pinnately compound leaves known as *Sapindopsis* from the Albian (upper Lower Cretaceous) of the Potomac Group of the eastern United States and of correlative strata elsewhere in the Northern Hemisphere displays a number of characters of form, venation, and margin which are consistent with primitive rosids. The earliest of these (*S. magnifolia* Fontaine) is pinnatifid with irregularly brochidodromous venation. Later forms, however, are truly pinnate and include members with teeth having secondary veins which branch near the sinus below the teeth, sending one branch to the tooth apex along the apical side of the tooth and the other into the area of the sinus or to the super-adjacent secondary. Although the shape and venation of these teeth is similar to that of the Cunonioid Tooth, a distinct spine or process at the tooth apex is unlike anything now found in the Rosidae. Some of these later *Sapindopsis* leaves also have laminar resin dots (Doyle & Hickey, in press).

Order 48. Saxifragales

Leaves basically pinnately compound; margin with Cunonioid Teeth; secondary veins semicraspedodromous; tertiary venation percurrent; laminar glands

absent; stipulate. (Excluding Paracryphiaceae which has modified but non-rosid teeth.)

Trends: 1. Leaves becoming palmately compound and palmately lobed in the Saxifragaceae and Grossulariaceae through inferred shortening of the pinnate rachis. 2. Leaves becoming simple in the Escalloniaceae, Hydrangeaceae, Iteaceae, and Pterostemonaceae. 3. Development of the Rosoid Tooth in the Saxifragaceae, Grossulariaceae, Escalloniaceae, Hydrangeaceae, and possibly others. 4. Development of a Spinose Tooth and pure craspedodromous venation in the Davidsoniaceae and Brunelliaceae. 5. Development of entire margins in Pittosporaceae and Bruniaceae. 6. Stipules lost in the Hydrangeaceae, Montiniaceae, Roridulaceae, Pittosporaceae, Byblidaceae, and Bruniaceae.

Order 49. Rosales

Leaves basically pinnately compound; margin with Rosoid Teeth having a clear glandular (hydathodal?) apical foramen; venation pinnate; secondary veins semicraspedodromous; tertiary venation transverse; laminar glands absent; stipulate.

Trends: To simple, entire leaves in the Chrysobalanaceae and to simple leaves with acropetiolar nectaries in the subfamily Prunoideae.

Order 50. Fabales

Leaves basically pinnately compound; margin entire; venation pinnate; secondary veins brochidodromous; stipules present.

Trends: Many and various with loss of leaflets, fusion of leaflets, and loss of the entire blade, among others.

Order 51. Connarales

Leaves pinnately compound; margin entire; exstipulate.

Order 55. Hippuridales

Leaves basically simple; margin with Rosoid Teeth; exstipulate.

Trends: 1. Leaves elliptic to linear with pinnate craspedodromous venation and Rosoid Teeth, or leaves reduced or filiform in the Haloragaceae. 2. Leaves simple, palmately lobed, with Rosoid Teeth and actinodromous venation in the Gunneraceae. 3. Leaves scale-like in the Hippuridaceae.

Order 25. Juglandales

Leaves pinnately compound; margin with Cunonioid Teeth; venation pinnate; secondary veins semicraspedodromous; tertiary venation percurrent; laminar glands resin secreting, sessile, stalked, capitate, and peltate; stipulate.

The presence of pinnately compound leaves having well developed Cunonioid Teeth make them anomalous in the Hamamelididae where they were placed by Takhtajan and Cronquist. Resinous secretions and peltate laminar glands similar to those in the Myricaceae and the Fagaceae occur abundantly in the rosid order Rutales. Although the wood anatomy of the Juglandales is more primitive than that of the Rutales, and workers such as Heimsch & Wetmore (1939) and Withner

(1941) have denied any strong relationship between the Juglandales and Rutales on this basis, similarities do exist (Handel-Mazzetti, 1932; Copeland & Doyel, 1940) which allow at least collateral derivation of the two lines. Such a scheme also requires that the tricolporate to triporate pollen and reduced inflorescences of Juglandales be convergent with the Betulaceae, Myricaceae, and Casuarinaceae, probably as independent adaptations to wind pollination rather than the result of common ancestry.

Trend: Loss of stipules in Juglandaceae.

Order 56. Rutales

Leaves basically pinnately compound; margin with Rosoid Teeth; venation pinnate; secondary veins semicraspedodromous; tertiary venation percurrent; laminar glands, resin secreting, sessile, stalked, capitate, and peltate; stipulate.

Trends: 1. Loss of marginal teeth resulting in a lamina whose secondaries are either eucamptodromous (Anacardiaceae) or rigidly brochidodromous (Burseraceae) and which turn upward abruptly near the margin. 2. Loss of laminar glands. 3. Loss of stipules.

Order 57. Sapindales

Leaves basically pinnately compound; margin with Cunonioid Teeth; venation pinnate; secondary veins semicraspedodromous; tertiary venation percurrent; stipulate.

Trends: 1. Development of palmately compound and palmately lobed leaves either through shortening of the pinnate rachis or loss of lateral leaflets. 2. Development of simple leaves. 3. Development of Spinose Teeth in *Meliosma*. However, present knowledge of the leaves of the Meliosmaceae is insufficient to allow their systematic placement. 4. Loss of stipules in families such as Aceraceae, Hippocastanaceae, and Meliosmaceae.

Order 58. Geraniales

Leaves pinnately compound; margin entire; venation pinnate; secondary veins camptodromous; tertiary venation percurrent; stipulate.

Trends: To simple leaves with petiolar attachments still persisting.

Order 59. Polygalales

Leaves simple; margin entire; venation pinnate; secondary veins brochidodromous; stipulate.

Trend: Loss of stipules.

Order 60. Cornales (including the Cornaceae, Garryaceae, Davidiaceae, Nyssaceae, Alangiaceae, and Mastixiaceae)

Leaves simple; margin with Rosoid Teeth; venation imperfectly actinodromous or acrodromous; tertiary venation percurrent; glands lacking; exstipulate.

Trends: Loss of teeth in Garryaceae, Alangiaceae, Mastixiaceae, and most Cornaceae and Nyssaceae.

Order 60A. Umbellales

Leaves pinnately compound to lobed; margin with Cunonioid Teeth (*Myodocarpus*); venation pinnate; stipulate with stipules sheathing part of the leaf base.

Trend: To palmately compound leaves having actinodromous venation and margins with Rosoid Teeth.

Order 62. Rhamnales

Leaves basically pinnately compound; margin with Cunonioid Teeth; venation pinnate; secondary veins semicraspedodromous; tertiary venation transverse; glands lacking; stipulate.

Trends: 1. The Leeaceae are pinnately compound with Cunonioid Teeth. 2. To simple, palmately lobed leaves with Rosoid Teeth; actinodromous primary venation and thick, moderately spaced, strongly percurrent tertiary veins (Vitaceae). 3. To simple leaves with Rosoid Teeth, pinnate venation and thin, closely spaced percurrent tertiary veins (Rhamnaceae).

Order 63. Oleales

Leaves basically pinnately compound; margin with Cunonioid Teeth; venation pinnate; secondary veins semicraspedodromous; tertiary venation percurrent; glands lacking; exstipulate.

Trends: 1. To simple leaves with craspedodromous secondary veins. 2. To Rosoid Teeth. 3. Loss of marginal teeth.

Order 66. Proteales

Leaves basically pinnately compound; venation pinnate; secondary veins semicraspedodromous; tertiary venation irregular; exstipulate.

Although basically pinnately compound, proteaceous leaves show no features which definitely relate them to the Rosidae.

Trends: 1. To simple leaves in both subfamilies of Proteaceae. 2. To ternately pinnatifid leaves, some with spinose tips, in the subfamily Proteoideae. 3. To Spinose Teeth and craspedodromous secondary venation in the subfamily Grevilleoideae.

Rosoid Tooth Types

1. *Cunonioid*—C (Figs. 2, 18)—Cunoniaceae, Leeaceae. Tooth with a small, clear glandular apex, with the principal vein to the tooth branching below it, in or near the sinus, and sending one branch to the superadjacent secondary vein or to the sinus and the other branch to the tooth apex on a deflected course along the apical side.

2. *Rosoid*—R (Figs. 2, 18)—Rosaceae, Saxifragaceae. Tooth with a large, clear glandular apical opening (foramen) broadening distally from the sub-apical termination of the usually central principal vein of the tooth. A pair of lateral accessory veins of higher order is connivent with the principal vein, follows a straight rather than a looped course, and terminates in the apical foramen. This tooth is generally broader and more symmetrical than the Cunonioid type.

3. *Spinose*—Sp (Fig. 18)—Meliosmaceae. Tooth with the principal vein projecting beyond its apex.

TABLE 2. Contrast in certain leaf characters between the Dilleniid Asteridae and the Rosid Asteridae. The cross stands for the presence of the named character; dashes for its absence; blanks for lack of data. In the columns where the letter symbols are not explained by the headings: P = pinnately lobed, C = Cunonioid Tooth type, P = pinnate vein configuration, Br = brochidodromous secondary veins, PAd = intercostal venation tending to be oriented parallel to the secondaries and ramifying admedially.

	LEAF CHARACTERISTICS								
TAXON	Simple / Compound	Pinnately Lobed	Entire / Toothed MARGIN	TOOTH TYPE	1° VEIN CONFIGURATION	2° VEIN CONFIGURATION	INTRAMARGINAL VEINS	INTERCOSTAL VENATION	LATEX
DILLENIID ASTERIDAE	S	--	E	--	P	Br	+	P Ad	+
GENTIANALES	S	--	E	--	P	Br	+	P Ad	+
POLEMONIALES	S	--	E	--	P	Br	+	P Ad	+
RUBIALES	S	--	E	--	P	Br	+	P Ad	
CAMPANULALES	S	--			P				+
ASTERALES	S	--	E	--	P	Br	+		+
ROSID ASTERIDAE	C	P	T	C	P				--
LAMIALES	S		T	C	P				--
SCROPHULARIALES	C	P	T	C	P				--
DIPSACALES	C	P	T	C	P				--

SUBCLASS G. ASTERIDAE

Although our survey of the leaves of the asterid families is as yet preliminary, our data indicate that the leaves of this subclass can be divided into two fundamental categories; one group most closely resembling the Ochnales-Myrtales (Fig. 12), which we call the Dilleniid-Leafed Asterids and the other most similar to those of Saxifragales-Araliales, which we term the Rosid-Leafed Asterids (Fig. 17). The basic leaf features of these two groups are summarized in Table 2 and in more detail below. The ordinal breakdown is that of Takhtajan with minor modifications after Cronquist. The status of stipules has not been analyzed in sufficient detail to determine whether they are basic to the orders or are of secondary origin within them; thus they have been omitted from consideration in this treatment.

I. DILLENIID-LEAFED ASTERIDS

Leaves basically simple; margin entire; venation pinnate; secondary veins strongly brochidodromous and tending to form an intramarginal vein (Fig. 19); intercostal venation tending to be oriented parallel to the secondaries, in ochnalean fashion; latex present (Table 2). In addition, this group tends to have interxylary phloem and vestured pits.

Order 68. Gentianales (excluding Rubiaceae after Cronquist, 1968)

Leaves simple; margin entire; venation pinnate; secondary veins brochido-

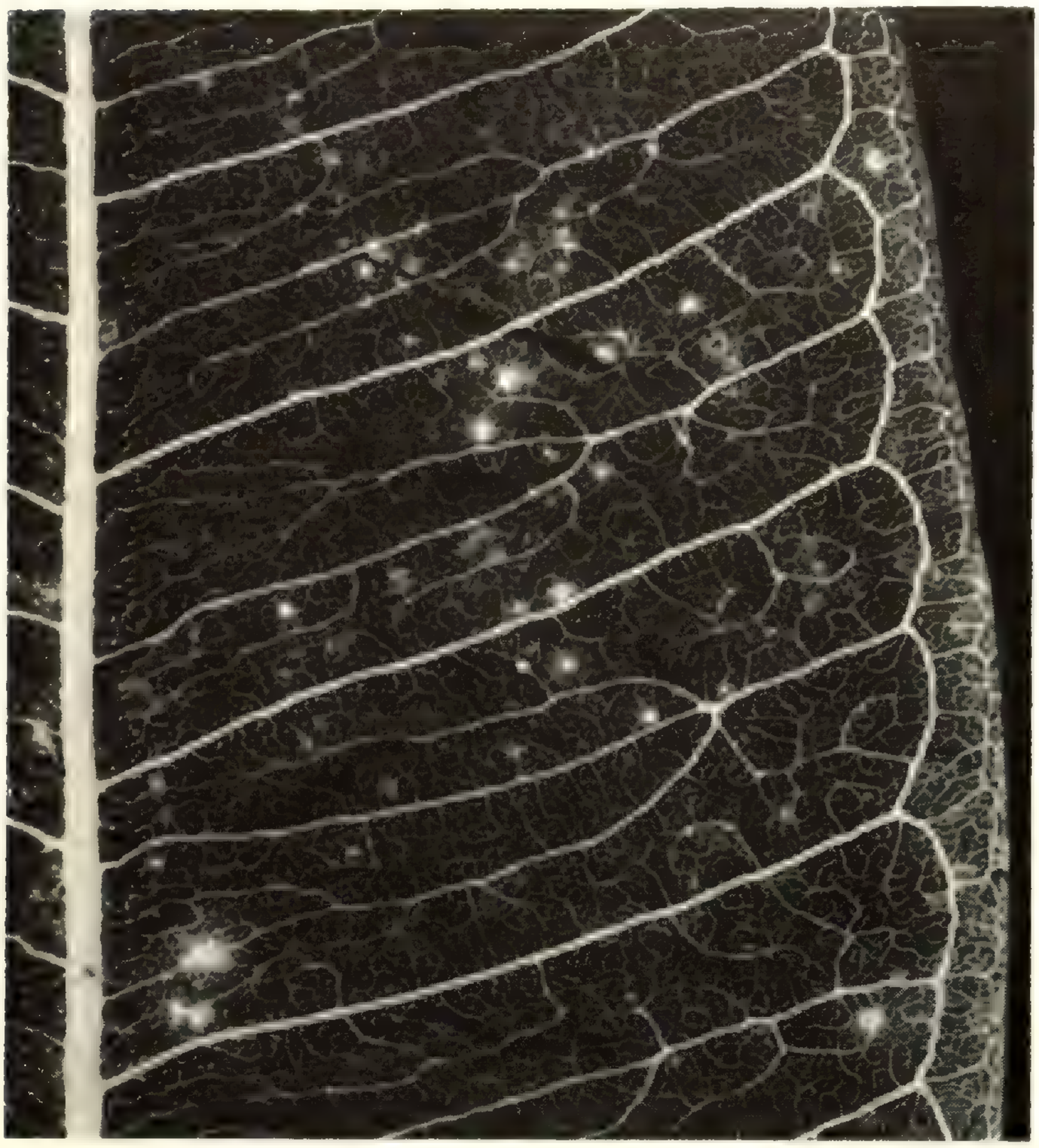


FIGURE 19. Ochnalean venation in the Gentianales; *Chilocarpus decipiens* Hook. (Apocynaceae); Sumatra: *Toroes 1428* (UC); × 5.

dromous, tending to form an intramarginal vein; tertiary venation tending to parallel the secondaries; latex present (Fig. 19).

Order 69. Polemoniales (including Solanaceae and Nolanaceae, after Cronquist, 1968)

Leaves simple; margin entire; venation pinnate; secondary veins strongly brochidodromous, tending to form an intramarginal vein; tertiary venation often paralleling the secondaries; latex very rare, known only in a few genera of the Convolvulaceae.

Order 69A. Rubiales (after Cronquist, 1968)

Leaves simple; margin basically entire; venation pinnate; secondary veins brochidodromous, tending to form intramarginal veins; tertiary venation oriented parallel to the secondaries; latex absent; stipulate.

Order 72. Campanulales

Leaves simple; margin entire; venation pinnate; secondary veins and higher order venation not determined for this study; latex present.

Order 74. Asterales

Leaves basically simple, when compound either pinnatifid or of pinnatifid origin by deeper dissection of an originally simple blade; margin entire; venation

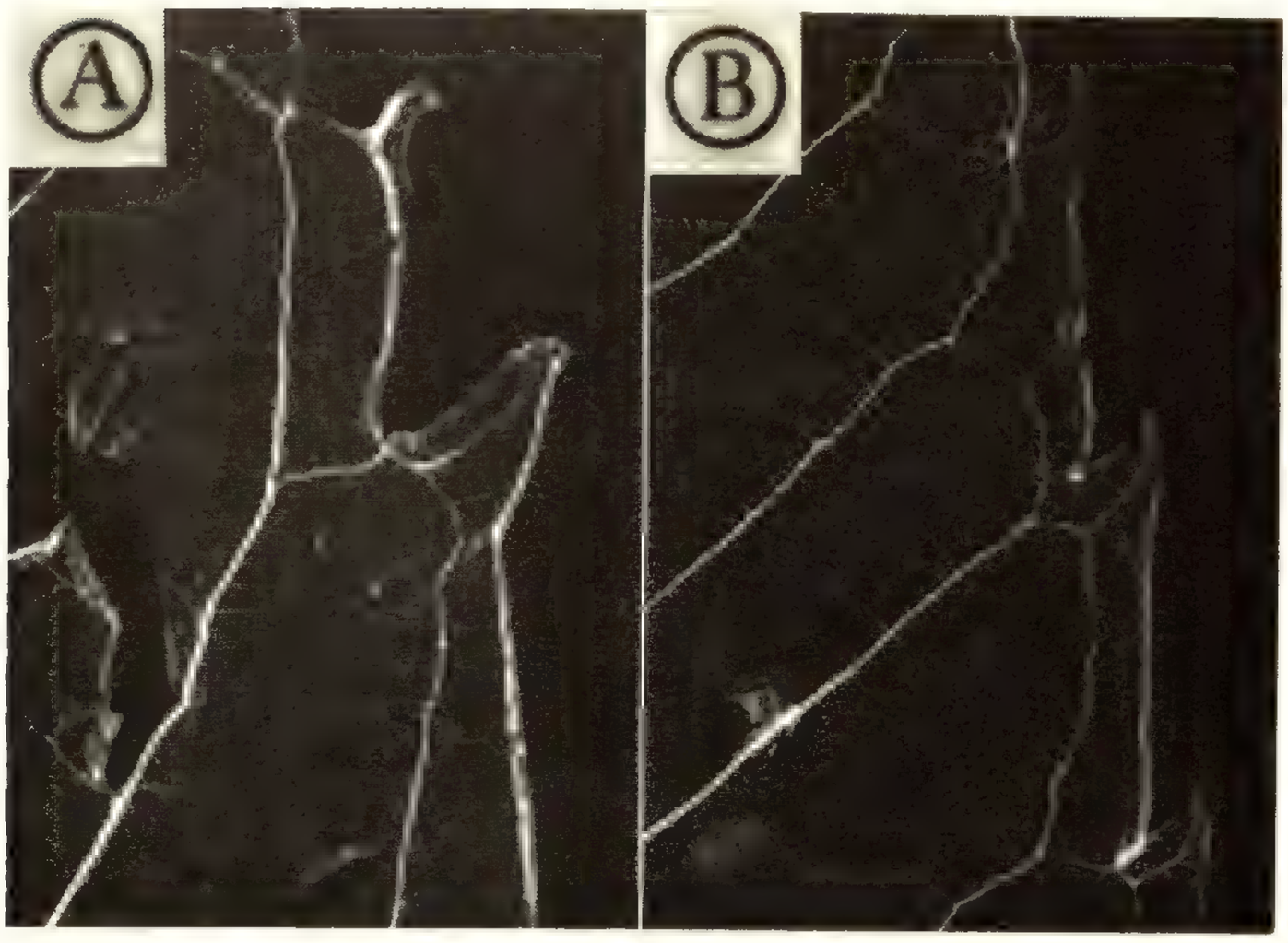


FIGURE 20. Inferred Cunonioid Teeth in the Scrophulariales; × 5.—A. *Tecoma stans* Juss. (Bignoniaceae); Nicaragua: *Smith s.n.* (UC 975382).—B. *Campsis chinensis* (Lam.) Voss. (Bignoniaceae); China: Kangsi, *Ip s.n.* (UC 258798).

pinnate; secondary veins brochidodromous and tending to form an intramarginal vein; tertiary venation various; latex present.

II. ROSID-LEAFED ASTERIDS

Leaves basically pinnately compound; margin with Cunonioid Teeth (Fig. 20); venation pinnate; secondary veins often semicraspedodromous; tertiary venation transversely ramified; latex absent. In addition interxylary phloem is absent except rarely in the Acanthaceae and very rarely in the Myoporaceae. Included phloem of the concentric type does occur in the Verbenaceae.

Order 67. Dipsacales

Leaves mostly simple except pinnately compound in *Sambucus* of the Caprifoliaceae; margin with Cunonioid and Rosoid Teeth; venation pinnate; secondary veins semicraspedodromous; tertiary venation transverse; latex absent.

Order 70. Scrophulariales (excluding Solanaceae and Nolanaceae after Cronquist, 1968)

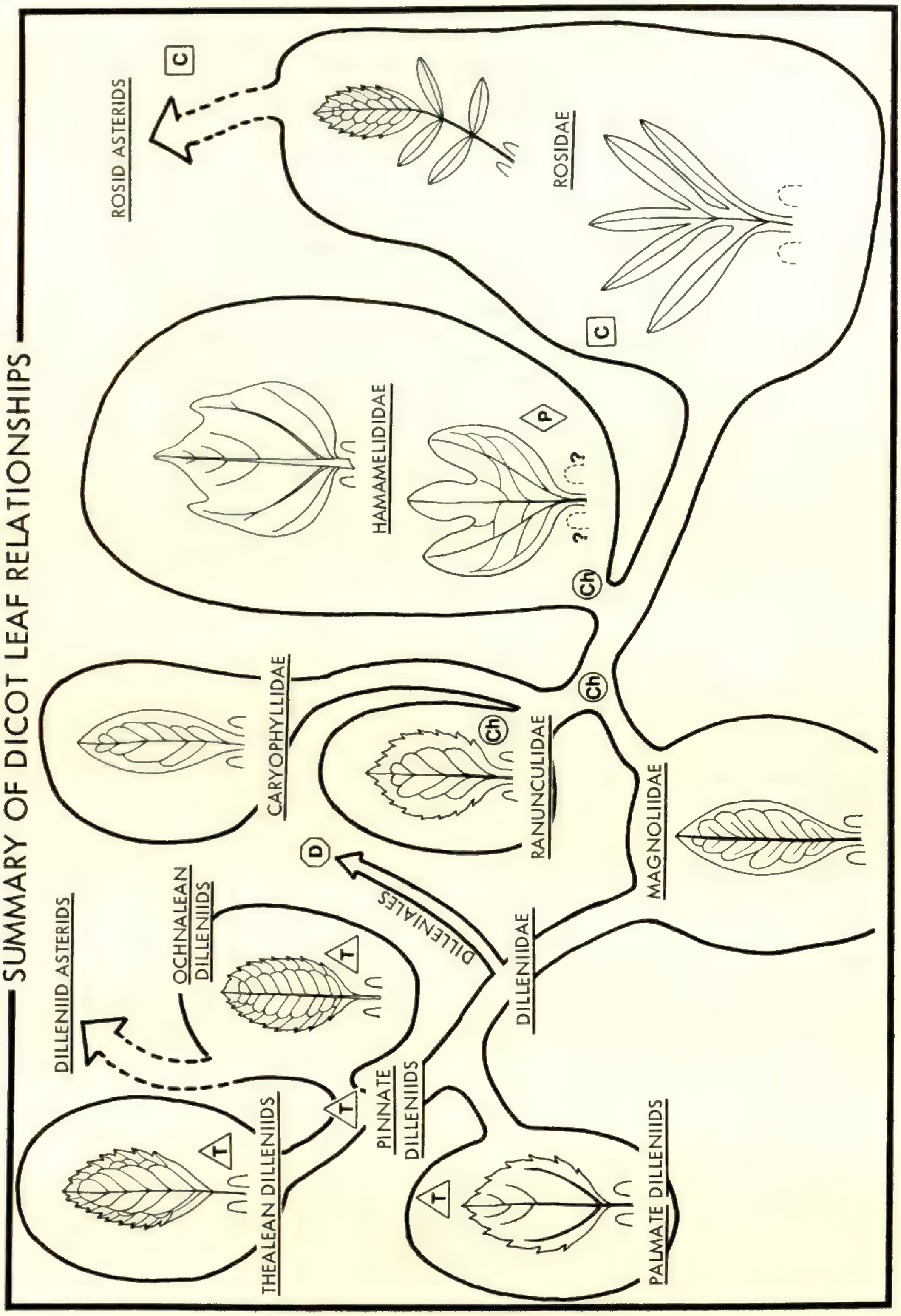
Leaves pinnately compound; margin with Cunonioid Teeth (Fig. 20); venation pinnate; latex absent.

Order 71. Lamiales

Leaves basically simple, margin with Cunonioid Teeth; latex absent.

CONCLUSIONS

The data which we have presented here demonstrate that a number of lower order leaf architectural features, including leaf organization, configuration of the first three vein orders, and characteristics of the leaf margin are significant sys-


SUMMARY OF DICOT LEAF RELATIONSHIPS
ROSID ASTERIDS
C
ROSIDAE
C
HAMAMELIDIDAE
P
?
?
Ch
CARYOPHYLLIDAE
Ch
RANUNCULIDAE
Ch
MAGNOLIIDAE
D
DILLENIALES
DILLENIIDAE
OCHNALEAN DILLENIIDS
T
THEALEAN DILLENIIDS
T
PINNATE DILLENIIDS
T
PALMATE DILLENIIDS
T
DILLENIID ASTERIDS

tematic indicators within the dicotyledons. We have shown that when variations in these characters are analyzed using the classifications of Takhtajan and Cronquist, they yield, with certain exceptions, a generally coherent arrangement, which we feel reflects the basic soundness of these classifications as approaches to a natural system.

Looking at their most obvious feature, dicot leaves display a rather general separation into four basic patterns of organization: simple, pinnately compound, palmately lobed, and palmately compound. However, when analyzed in terms of the Takhtajan and Cronquist systems and in conjunction with variation in their vein configuration and marginal features, each of these forms can be seen to have arisen several times. Each line, however, often retained characteristics which betray these separate origins (Fig. 21). Thus simple leaves are found in the Magnoliidae, Caryophyllidae, Pinnate Dilleniidae, the so-called "Dilleniid-Leafed Asterids," as well as in the other subclasses, as reductions of the compound condition. However, the affinities of the simple leaves in each of these subclasses can be recognized by a combination of higher order architectural features such as vein disorganization or the presence of intersecondaries in the Magnoliidae, obsolescence of venation above the fourth order and a trend to imperfect actinodromy or acrodromy in the Caryophyllidae, or by a characteristic tooth type and course of the secondary and tertiary venation in the other subclasses. Pinnately compound leaves seem to have developed separately in both the Ranunculidae and the Rosidae, the distinction between them being in their respective tooth types and primary and secondary venation. Palmately lobed leaves are seen in the Hamamelididae, the Palmate Dilleniidae, and in the Rosidae, the basic differences in venation and characters of the marginal teeth showing the fundamental separation of these taxa. Palmately compound leaves are known principally in the Palmate Dilleniidae, less often in the Rosidae and only very rarely in the Hamamelididae.

Apparent also from the preceding survey is the stability of many of the tooth types found in dicot leaves. Recognition of these tooth types thus appears to be an overlooked tool of major systematic importance. Of the various types, the Chloranthoid Tooth in the Ranunculidae, certain Magnoliidae, and some of the Hamamelididae; the Theoid Tooth in the Dilleniidae; and the Cunonioid Type in the Rosidae are the most important. Classification of tooth type is of great significance in the systematic recognition of leaves at higher taxonomic levels, and the determination of a number of characteristic variations in tooth type

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FIGURE 21. Summary of dicot leaf relationships. Basic leaf types of the various subclasses are indicated by the drawings. Note that only the Rosidae and the Rosid Asterids have basically pinnately compound leaves and that the Asteridae have two apparently separate leaf affinities. The Dilleniales are shown as an early and isolated offshoot of the Dilleniid stock distantly related to its later elaboration. The basal leaf in the Hamamelididae represents the Cretaceous fossil group termed the "Platanoids" and the pinnatifid leaf in the Rosidae represents the middle Cretaceous genus *Sapindopsis*, which possibly has affinities to the basal Rosidae. Basic tooth types shown are: Ch = Chloranthoid, P = Platanoid, C = Cunonioid, D= Dillenioid, T = Theoid.

appears to be an important key in ascertaining patterns of evolution in the various groups.

The persistence and stability of these tooth types through extensive taxonomic reaches of the dicotyledons has further and rather unexpected implications for the determination of angiosperm evolution. Work by Sinnott & Bailey (1915), Bailey & Sinnott (1916), Chaney & Sanborn (1933) and Wolfe (1971) showed that the great majority (75–90%) of tropical rainforest leaves have entire margins. This percentage decreases to near equality in the upland tropics and subtropical forests, while the leaves of temperate forests are mainly non-entire. Leaves of arctic, alpine, and xeric environments are predominately entire-margined.

Our observation of the persistence and coherence of tooth evolution patterns from a portion of the Magnoliidae and into the Ranunculidae, Hamamelididae, Dilleniidae, Rosidae, and possibly what we have called the "Rosid-Leafed Asteridae" (Fig. 21), may indicate that most of the important innovations in dicot radiation leading to major shifts in adaptive strategy could not have taken place in a setting analogous to that of the present tropical rainforest. It seems possible that in the rainforest setting the survival of microscopic adaptations and the process of extreme niche partitioning have given rise to a great diversity of species, but the region may, in general, be a "phyletic sink" compared to more extreme humid climatic regions. In more extreme environments a premium on macroscopic adaptation may result in more radical shifts in adaptive strategies leading more rapidly to novelty at higher taxonomic levels. An exception to this picture is, of course, the Ochnalean Dilleniid Alliance where teeth seem to be lost near the base of the line.

This analysis also resolves the assignment of certain taxa about which there is doubt or disagreement between the treatments of Takhtajan and Cronquist. For example, due to its basically pinnately compound leaf form the Ranunculidae are retained as a separate subclass as by Takhtajan (1969), but the Illiciales, with simple leaves, are moved to the Magnoliidae as by Cronquist (1968).

Leaf data also appear to support Takhtajan's assignment of the Euphorbiales to the Dilleniidae. Leaves reinforce Cronquist's assignment of the Lecythidaceae and related families to the Dilleniidae, rather than to the Rosidae as in Takhtajan; the erection of two orders for Takhtajan's (1969) order Cornales; and the assignment of the Solanaceae to the Polemoniales rather than to the Scrophulariales, as by Takhtajan. In addition, our analysis suggests the reassignment of several "problem" families like Didymelaceae to the Dilleniidae, as well as reinforcing the assignment of the Medusagynaceae to that subclass by both authors.

On the other hand, certain areas where the leaf data are anomalous in the light of the Takhtajan and Cronquist systems should lead to a careful reevaluation of all morphologically and systematically significant features and of the assumptions of the systems themselves in order to resolve the conflicts. The most important of these are our reassignment of the Juglandales to the Rosidae, the strong leaf architectural affinities of the Celastrales and Myrtales to the Pinnate-Leafed Dilleniidae, and the apparent fundamental separation of the leaf architectural patterns of the Asteridae into two groups, one having Ochnalean-Myrtalean leaf affinities and the other having an apparent Rosid pattern. Numerous other

leaf groupings which we have made at lower taxonomic levels must be similarly evaluated.

For the purpose of a comparison of leaf architectural features with degree of phylogenetic advancement, we take as our assumption, as Takhtajan and Cronquist did, that the Magnoliidae as a whole represent a residuum of the most primitive features among the living dicots. Starting from this, the simple, entire, pinnately-veined leaf with somewhat irregular camptodromous secondary venation, and irregular tertiary and high order veins appears to be most primitive among living leaves; and the non-entire, lobate, and compound leaf appears to be more advanced. This observation accords with Lower Cretaceous fossil evidence of dicot evolution reviewed by Doyle & Hickey (in press).

Finally, this paper provides the first framework for a systematic summary of dicot leaf architectural features and for the development of a regular systematic method for their identification. Not only will this be of importance for the determination of modern leaves but will also make possible the identification of dicot leaf fossils at higher taxonomic levels, thus leading to significant contributions in deciphering the phylogeny of angiosperms from their fossil remains.

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THE BASES OF ANGIOSPERM PHYLOGENY: VEGETATIVE ANATOMY[1]

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ABSTRACT

The principal characters of vegetative anatomy which are of phylogenetic significance at the higher levels in angiosperm systematics are defined and discussed in relation to their taxonomic distribution in the Takhtajan and the Cronquist systems of angiosperm classification. In absence of a complete fossil record, application of the phylogenetic method of association, correlation, and common ground plan are illustrated from anatomical data. Vegetative structure contains a wealth of potentially significant systematic information. However, only the evolutionary trends in the secondary xylem and the phylogenetic conclusions that have resulted from recognizing these trends, provide a firm basis of angiosperm phylogeny. In order for the phylogenetic significance of other vegetative anatomical characters to be fully realized, more comprehensive studies must be undertaken and new methodologies and approaches applied. For the most part, anatomical data support the phylogenetic conclusions of the Takhtajan and Cronquist systems of angiosperm classification at the higher taxonomic levels. However, the most reliable application of anatomical information remains in statements of negation of close relationship rather than positive assertions of close affinity.

Anatomical characters have been employed for systematic purposes well over a hundred years. C. R. Metcalfe (1968) has stated that anatomy of the vegetative organs of flowering plants can be taxonomically useful in the following ways: (1) The identification of fragmentary material, (2) the preliminary identification of herbarium specimens, and (3) as an aid toward establishing the interrelationships of taxa at and above the species level. It is important, accordingly, to initially make the distinction between general (diagnostic) taxonomic characters that enable a genus or species to be separated and distinguished from other plants, and characters that assist in our understanding the evolutionary relationships of plants. The primary intention of this paper is to identify the techniques and major characters of vegetative anatomy that form a basis of angiosperm phylogeny at the higher taxonomic levels and how these characters relate to the general systems of angiosperm classification recently proposed by Cronquist (1968) and Takhtajan (1969). Characters of potential phylogenetic significance in angiosperms as a whole and the taxonomic distribution of these characters at different levels in the taxonomic hierarchy are treated. Finally, an attempt is made to evaluate the present state of systematic anatomy and consider what contributions vegetative anatomy may be able to provide in the future with regards to angiosperm phylogeny. Unless indicated otherwise, terms are defined in accordance with Esau (1961).

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Technique

The discipline of systematic anatomy is fundamentally descriptive, with comparative data usually obtained from material that has been fixed, sectioned, and stained for microscopical examination and subsequently placed in a reference slide collection. However, temporary preparations of petioles and nodes using freehand procedures can yield rapid data with satisfactory results. Quantitative methods (i.e., statistical correlations) have proven most applicable to the secondary xylem and were the principal tools used in elucidating the major trends of evolution in this tissue. It is manifest that any consideration of the geologic histories of plants should rely heavily on the fossil record. To date, only the secondary xylem of fossil angiosperms has revealed significant phylogenetic information, although, as seen elsewhere in this volume, the fossil record is becoming more useful in regards to other plant structure. Ontogenetic evidence has been employed on occasion and is becoming increasingly valuable.

In recent years, the assumption that a single sample of an organ or tissue provides reliable data upon which to base anatomical generalizations has been shown to be invalid. It is essential, therefore, that the ranges of variability of anatomical characters within the same individual and different individuals in relation to the environment, location of tissues within the plant, and ontogeny be thoroughly investigated. Admittedly, it is often impossible for the comparative anatomist to obtain adequate materials for such studies. However, the goal of all anatomical research should be to make each investigation as comprehensive as possible, and in this vein, Carlquist (1961) has stressed the need to describe the entire range of character variation, or "complement," of a given tissue or structure. A major difficulty the comparative anatomist confronts is distinguishing characters of diagnostic, phylogenetic, and ecological significance. At our present state of knowledge, it is often not possible to separate evolutionary advancement for ecological modification.

The selection of material for study is very critical. It is known, for example, that the first-formed secondary xylem may differ histologically from later-formed wood and thus the uniform selection of mature samples for comparative purposes is desirable. Unfortunately, a large amount of wood data in Solereder's (1908) book were derived from young twigs. Another shortcoming of much early systematic anatomical work was the lack of concern for voucher specimens. It is of utmost importance that the specimens investigated be correctly identified or at least available for taxonomic scrutiny. Without documenting specimens, the value of the anatomical method is considerably reduced. The role of wood collections as bases for research in plant systematics and evolution has been reviewed by Stern (1973) and Wetmore et al. (1974).

In a discussion of phylogeny the terms primitive and advanced with respect to different character states cannot be avoided. Sporne (1948) used the term "primitive character" to mean one which is possessed by a present day taxon and was also possessed by its ancestors. An "advanced character," on the other hand, is one possessed by a present day taxon and not possessed by its ancestor, that is, it replaced an ancestral character during evolution. A fundamental problem confronted by comparative anatomists involved in phylogenetic pursuits is to

determine the direction in which structural modifications have occurred or are occurring, i.e., to identify primitive and advanced characters within the taxonomic units under study, and to determine whether this direction has reversed (Cheadle & Tucker, 1961). Because the erratic fossil record is of little assistance in this regard, other approaches must be employed (see Sporne, 1956). The most successful methods as related to comparative anatomy are termed by Sporne (1956) the doctrines of association, correlation, and common ground plan. Examples of the application of these methods are presented throughout this paper.

That vessel elements evolved from tracheids is certain. Advantageously, the sequence involves characters that are measurable, and, therefore, can be dealt with statistically. Bailey & Tupper (1918) provided the earliest systematic evidence for this trend in a comparison of length of tracheary elements of vascular cryptogams, gymnosperms, and angiosperms. Frost (1930a, 1930b, 1931) extended this work and initiated a detailed statistical analysis of specialization of the secondary xylem in dicots. Frost made two basic assumptions that could be proved by subsequent tests of association and correlation. The first was that the primitive state of the derived structure will resemble the ancestral structure if it can be determined from which structure the other evolved. Since it was assumed that vessel elements evolved from tracheids, Frost deduced that the most primitive vessel elements were those which most resembled tracheids (doctrine of association). If this were not true, then the assumption of a direct relationship is incorrect, or the structures are so widely separated in the evolutionary scale that the tracheid-like condition of the vessel element has been lost. The doctrine of association has been criticized because of assumptions that are made prior to its application. Frost's second assumption, the doctrine of correlation, takes advantage of the fact that primitive characters are frequently associated with other primitive characters. Thus, if one character can be demonstrated to be primitive (e.g., scalariform perforation plates on the vessel end wall), then characters correlated with this feature are probably also primitive. The doctrine of the common ground plan assumes that any character present in all individuals of a taxon, or the most common character state among a group of related plants, must be the ancestral or primitive state.

Phylogenetic speculation involving the concepts of tissue conservatism, recapitulation of phylogeny during ontogeny, and teratology generally have met with criticism and limited success.

MAJOR REFERENCE WORKS

Systematic anatomy had its beginnings in the middle 1800's with the contributions of Sanio, Radlkofer, Vesque and others. Application of the anatomical method toward the solution of systematic problems was strongly advocated by Fritsch (1903) and thoroughly reviewed by Metcalfe (1946, 1953, 1954, 1959, 1961), whose thoughts have been freely drawn upon in the preparation of this paper. The first comprehensive, systematic summary of anatomical information was provided by Hans Solereder whose *Systematic Anatomy of the Dicotyledons* (2 vols.) was published in English translation in 1908. These landmark volumes provided the basis of all subsequent work on comparative vegetative anatomy

and are still indispensable reference sources. In 1950 a monumental two volume work *Anatomy of the Dicotyledons*, by C. R. Metcalfe and L. Chalk appeared, again dealing with aspects of vegetative anatomy, although emphasizing wood structure as a systematic and phylogenetic tool. The authors' objectives were ". . . to write this book in the hope that a modern counterpart to Solereder's well-known treatise on the same subject would lead towards a more natural classification of the Dicotyledons and make some contributions to our knowledge of phylogeny." Interestingly, as late as 1950, our knowledge of dicotyledonous vegetative anatomy could still be contained in only two volumes. Work is currently underway in the Jodrell Laboratory at Kew on a revision of this book.

Reference sources on the anatomy of monocotyledons begin with Solereder and Meyer's never completed *Systematische Anatomie der Monokotyledonen* published between 1928 and 1933. Quite recently, a series dealing exclusively with vegetative anatomy entitled *Anatomy of the Monocotyledons* has begun to appear under the editorship of C. R. Metcalfe. The subjects, authors, and dates of publication of completed books are as follows: Vol. I, Gramineae by C. R. Metcalfe (1960); Vol. II, Palmae by P. B. Tomlinson (1961); Vol. III, Commelinales-Zingiberales by P. B. Tomlinson (1969); Vol. IV, Juncales by D. F. Cutler (1969); Vol. V, Cyperaceae by C. R. Metcalfe (1971); and Vol. VI, Dioscoreales by E. S. Ayensu (1971).

Also worthy of mention as a reference source is the *Handbuch der Pflanzenanatomie* that was edited in the first edition by K. Linsbauer and is now being published in the second edition as the *Encyclopedia of Plant Anatomy*. Careful attention should also be given to *Comparative Plant Anatomy* by Carlquist (1961).

Principal Characters of Phylogenetic Significance

Secondary Xylem

During the past fifty years the value of wood anatomy, and vessel element evolution in particular, in the study of the phylogeny and classification of angiosperms has been clearly established. In no other vegetative tissues of the plant are the trends of evolution as clearly defined. These trends were recognized entirely without reference to existing taxonomic systems and thus without reference to the relative primitiveness or advancement of the plants in which they occur. The many achievements of wood anatomy in this repect have been subjects of several reviews (Chalk, 1937, 1944; Tippo, 1946; Vestal, 1940; Carlquist, 1961) and have perhaps tended to present vegetative anatomy in a rather one-sided manner. Bailey (1951) and Metcalfe (1954), among others, have noted that a phenetic classification of the dicotyledons, reflecting levels of evolutionary advancement, could be constructed entirely from anatomical information. Such a classification would be extremely difficult, if not impossible, to construct if vegetative characters exclusive of wood were considered. The vast amount of comparative data on wood structure results in part from the economic importance of wood, the relative ease of specimen preparation, and the fact that secondary xylem is often well preserved in herbarium specimens and fossil materials as a result of rigid cell walls. Major wood characters of proven phylogenetic value

are outlined and discussed below. Terms are defined in accordance with the *Multilingual Glossary of Terms Used in Wood Anatomy* (Committee on Nomenclature, 1964).

I. Tracheids and fibers (imperforate tracheary elements).
   A. Types.
      1. Tracheid. An imperforate wood cell with bordered pits to congeneric elements (Figs. 3e–f).
      2. Vasicentric tracheid. A short, irregularly-formed tracheid in the immediate proximity of a vessel and not forming part of a definite axial row (Fig. 3p).
      3. Fiber. A general term of convenience in wood anatomy for any long, narrow cell of wood or bast other than vessels and parenchyma. Note: often further qualified as wood fibers or bast fibers; the former including both the tracheids of gymnosperms and libriform wood fibers and fiber-tracheids of wood angiosperms. Also used loosely for wood elements in general.
      4. Fiber-tracheid. A fiber-like tracheid; commonly thick-walled with a small lumen, pointed ends, and bordered pit pairs having lenticular to slit-like apertures. This term is applicable to the late wood tracheids of gymnosperms as well as to the fiber-like tracheids of woody angiosperms (Figs. 3b–d).
      5. Libriform wood fiber. An elongated, commonly thick-walled cell with simple pits; usually distinctly longer than the cambial initial as inferred from the length of vessel members and parenchyma strands (Fig. 3a).
      6. Septate wood fiber. A fiber with thin transverse walls across the lumen (Fig. 3o).
   B. Wall thickness, sculpture, and cell length. Wall thickness ranges between very thin (lumen much greater than thickness of wall) and very thick (lumen almost completely closed). Element length ranges between very short (up to 1000 μm) and very long (over 2000 μm). Elements may have spiral thickenings that are helical ridges on the inner face of, and part of, the secondary wall.

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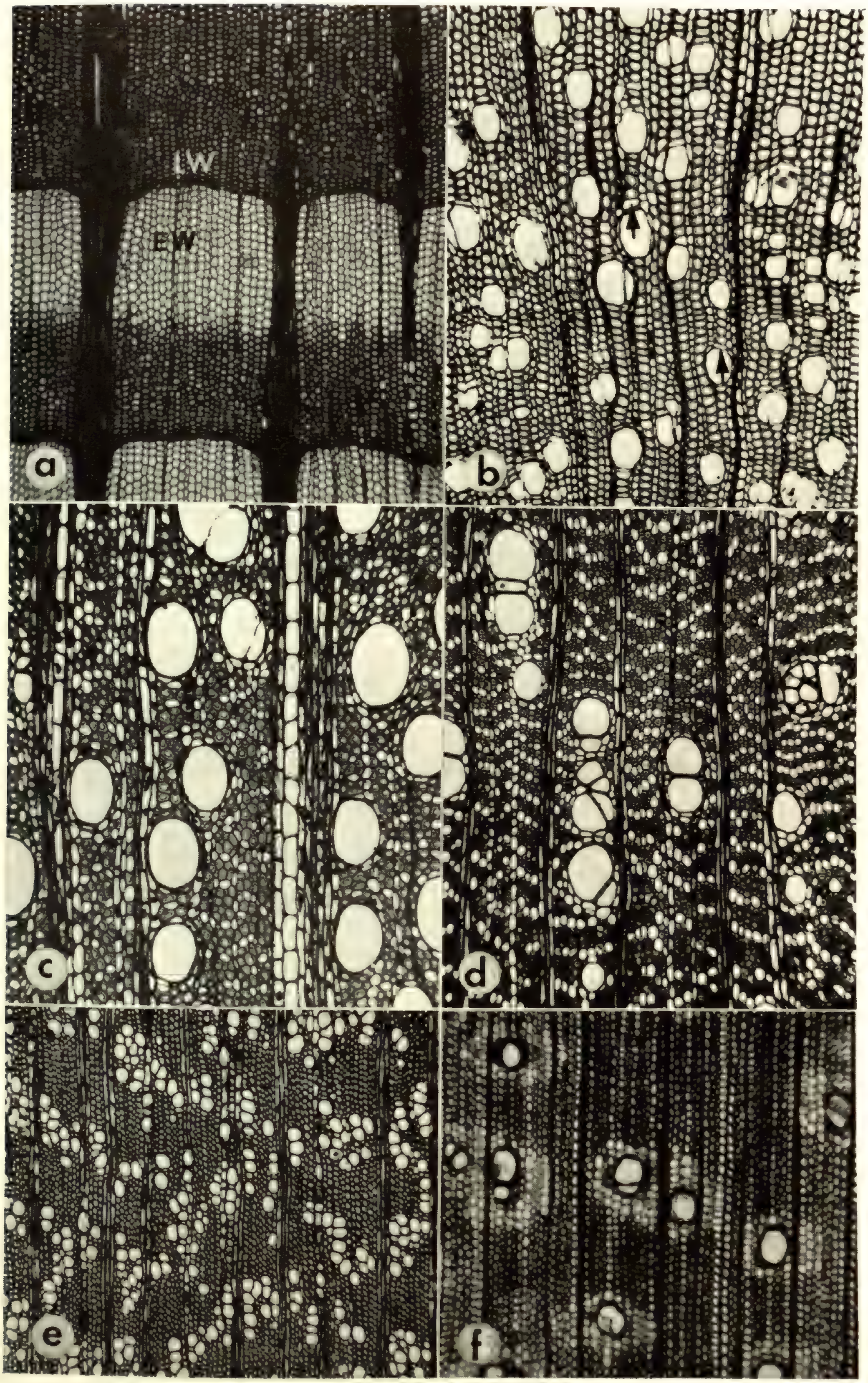
FIGURE 1. Transverse sections of dicotyledonous woods.—a. *Trochodendron aralioides* (Trochodendraceae), a primitively vesselless angiosperm showing the secondary xylem composed of tracheids. Distinction can be noted between tracheids of the late-wood (LW) and early-wood (EW); × 46.—b. *Schumacheria castaneifolia* (Dilleniaceae). This wood shows solitary, angular vessels and mostly scanty axial parenchyma (arrows). The imperforate tracheary elements are fiber tracheids; × 55.—c. *Dillenia pentagyna* (Dilleniaceae). Although this wood still has a comparatively primitive structure, the vessels are more rounded in outline and the axial parenchyma is both paratracheal scanty and apotracheal diffuse to diffuse-in-aggregates; × 55.—d. *Scytopetalum tieghemii* (Scytopetalaceae). In this wood the vessels are distributed as solitary pores and pore multiples. Imperforate tracheary elements are thick-walled libriform fibers and axial parenchyma is mostly diffuse-in-aggregates; × 55.—e. *Pittosporum tenuifolium* (Pittosporaceae). Note the pores are distributed in pore chains and radial pore multiples; × 55.—f. *Paulownia tomentosa* (Scrophulariaceae). Note the vasicentric parenchyma; × 46.


LW
EW
a
b
c
d
e
f

II. Vessels (perforate tracheary elements). A vessel is an axial series of cells (vessel members or elements) that have coalesced to form an articulated tube-like structure of indeterminate length; the pits to congeneric elements are bordered.

A. Pore (vessel) distribution.

1. Solitary pores. A pore completely surrounded by other elements (Figs. 1b–c).
2. Pore chain. A series or line of adjacent solitary pores (Fig. 1e).
3. Pore multiple. A group of two or more pores crowded together and flattened along the lines of contact so as to appear as subdivisions of a single pore. The most common type is a radial pore multiple, in which the pores are in radial files with flattened tangential walls between them (Fig. 1d). Another type is a pore cluster, in which the grouping is irregular.

B. Vessel element shape, wall thickness, and size. Vessel outline as seen in transverse section ranges from angular (Fig. 1b) to circular (Fig. 1d), with variation from thin to thick walled. Pore diameter as measured in transverse section ranges between extremely small (up to 25 μm) to extremely large (over 400 μm). Length of vessel elements as recorded from tip to tip range from extremely short (less than 175 μm) to extremely long (over 1900 μm).

C. Perforation plates. A perforation plate is a term of convenience for the area of the wall (originally imperforate) involved in the coalescence of two members of a vessel. Principal types of perforation plates are scalariform and simple. A scalariform plate has multiple perforations elongated and parallel (Fig. 3g). The remnants of the plate between the openings are called bars. Significant variations include the number of bars and whether the perforations are completely bordered (Fig. 3g), bordered to the middle, bordered at the ends (Fig. 3h), or non-bordered. A simple perforation plate consists of a single and usually large and more or less rounded opening in the perforation plate (Fig. 3k). Perforation plate end walls range from highly oblique to transverse (Figs. 3g–k).

D. Intervascular pitting. A term used (a) in a wide sense for pitting between tracheary elements, and (b) in a narrower sense in wood anatomy for pitting between vessel members.

1. Scalariform. Pitting in which elongated or linear pits are arranged in a ladder-like series (Fig. 3g).
2. Opposite. Multiseriate pitting in which the pits are in horitizontal pairs or in short horizontal rows (Figs. 3h–i). Note: when pits are crowded, the outlines of the borders tend to become rectangular in surface view.
3. Alternate. Multiseriate pitting in which the pits are in diagonal rows (Figs. 3j–k).

III. Rays. A ray is a ribbon-like aggregate of cells extending radially in the xylem and phloem. Xylem rays are classified on the basis of type and size.

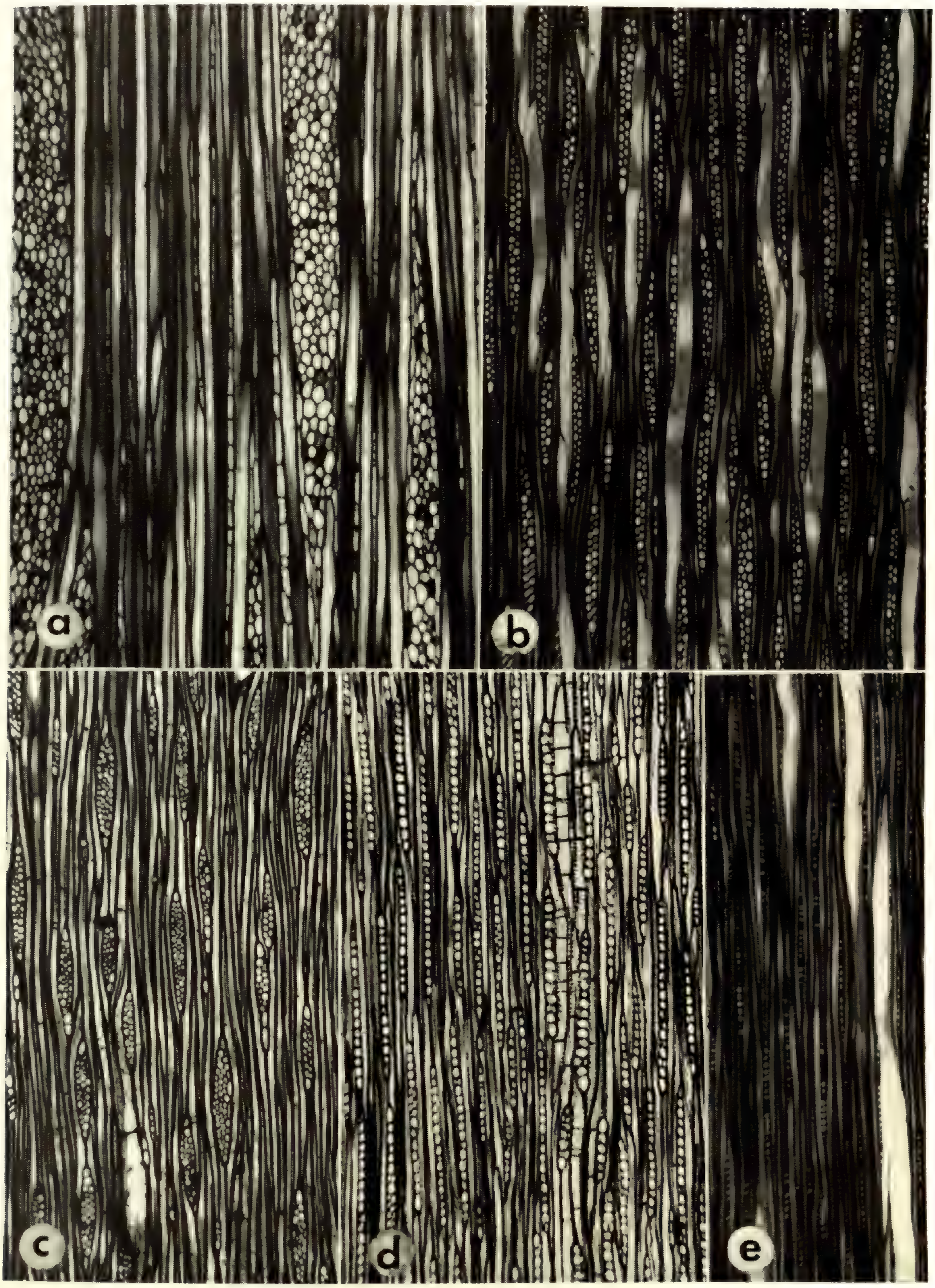


FIGURE 2. Tangential sections of dicotyledonous woods.—a. *Bubbia semecarpoides* (Winteraceae). Note primitive ray histology in this wood. Both heterocellular multiseriate and uniseriate rays are present; × 46.—b. *Magnolia grandiflora* (Magnoliaceae). This wood shows both uniseriate and multiseriate (biseriate) heterocellular rays. The uniseriate wings on the multiseriate rays are often reduced to a single cell; × 46.—c. *Pittosporum kauaiense* (Pittosporaceae). Rays are heterocellular with multiseriate body of the rays composed predominately of procumbent cells; × 55.—d. *Gonystylus warburgianus* (Thymelaeaceae). The rays of this species are predominately uniseriate and nearly homocellular; × 55.—e. *Populus deltoides* (Salicaceae). Note the exclusively uniseriate and homocellular rays; × 46.

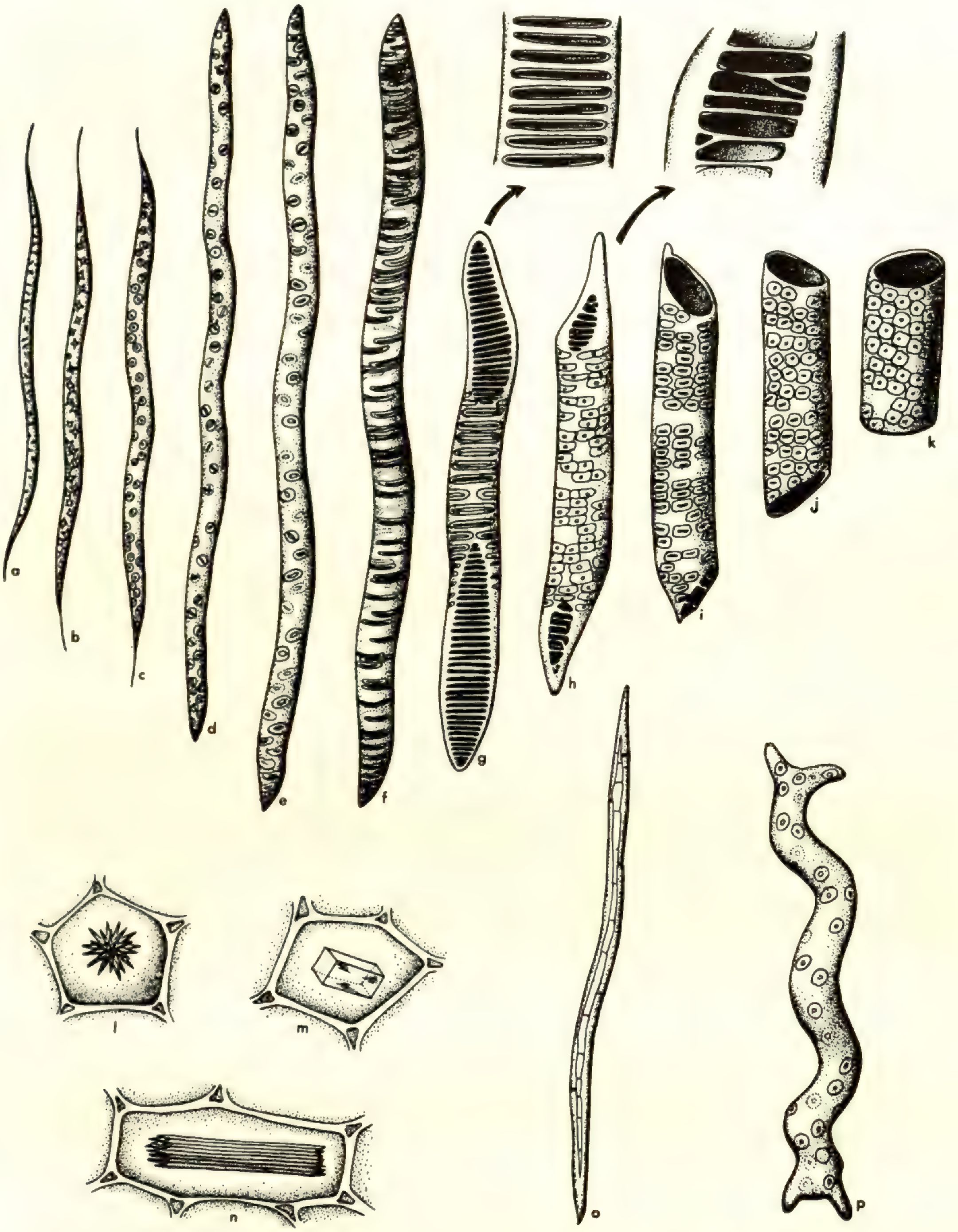


FIGURE 3. Cell types of the secondary xylem.—a–d. Wood fibers.—a. Libriform wood fiber. Note the simple pit and pointed ends of this most advanced of wood fiber types.—b–d. Fiber-tracheids. Note the progressive loss of the pit border from d to b.—e–f. Tracheids. The cell figured in e has circular-bordered pits whereas the element pictured in f has scalariform pits. —g–k. Vessel elements.—g. The cell pictured here represents a primitive vessel element type with many-barred scalariform perforation plates that are fully bordered (inset) and scalariform intervascular pitting.—h. This cell also has scalariform perforation plates but the number of bars is reduced in number and they are bordered only at the ends (inset). The intervascular pitting is multiseriate and arranged in an opposite manner.—i. This vessel element represents an

With respect to type, rays are heterocellular and homocellular. A heterocellular ray is one in which the individual rays are composed of both procumbent cells and square or upright cells (Figs. 2a–c), whereas a homocellular ray is composed wholly of cells of the same morphological type, i.e., all procumbent or all square or upright (Fig. 2e). With respect to size, rays are described as uniseriate if they are one cell wide as seen in tangential section (Figs. 2d–e), and multiseriate if they are more than one cell wide (Figs. 2a–c). Ray height is generally recorded in terms of the number of cells.

IV. Axial parenchyma. Parenchyma cells derived from fusiform cambial initials. Axial parenchyma distribution (as seen in transverse section) is classified in the following way.
   A. Apotracheal parenchyma. Axial parenchyma typically independent of the pores or vessels.
      1. Terminal parenchyma. Apotracheal parenchyma cells occurring either singly or forming a more or less continuous layer of variable width at the close of a season's growth.
      2. Diffuse parenchyma. Single apotracheal parenchyma strands or cells distributed irregularly among fibers (Fig. 1c).
      3. Diffuse-in-aggregates. Apotracheal parenchyma cells that tend to be grouped in short tangential lines from ray to ray (Figs. 1c–d).
      4. Banded apotracheal parenchyma. Axial parenchyma forming concentric lines or bands. Note: termed apotracheal banded, if typically independent of the vessels; paratracheal banded, if associated with the vessels.
   B. Paratracheal parenchyma. Axial parenchyma associated with the vessels or vascular tracheids.
      1. Scanty parenchyma. Incomplete sheaths or occasional parenchyma cells around the vessels (Figs. 1b–c).
      2. Vasicentric parenchyma. Paratracheal parenchyma forming a complete sheath around a vessel, of variable width and circular or slightly oval in cross section (Fig. 1f).
      3. Aliform parenchyma. Paratracheal parenchyma with wing-like lateral extensions, as seen in cross section.
      4. Confluent parenchyma. Coalesced aliform parenchyma forming irregular tangential or diagonal bands, as seen in cross section.

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intermediate stage in evolution with a scalariform perforation plate at one end and a simple perforation plate at the other end. Intervascular pitting is still essentially opposite.—j. The cell pictured here is further advanced as evidenced by the exclusively simple perforation plates that are tending to become transverse in orientation. The intervascular pitting is best described as transitional between opposite and alternate.—k. This vessel element is the most advanced type illustrated, with simple, transverse perforation plates and alternate intervascular pitting. Also note its short length and increase in width.—l–n. Crystal types.—l. Druse.—m. Prismatic form. —n. Raphides.—o. Septate libriform wood fiber.—p. Vasicentric tracheid. Note the irregular shape of this element. (From A. E. Radford, W. C. Dickison, J. R. Massey & C. R. Bell. Vascular Plant Systematics. Copyright 1974 by Harper & Row, Publ. Used with permission.)

The trends of evolution of the vessel element have been firmly established through extensive and intensive comparative anatomical studies on both fossil and living material, statistical analyses (i.e., measurements and correlations), and ontogenetic studies. Therefore, the evolutionary trend from tracheids to vessel elements is the most reliable tool known in the study of phylogeny. This is true because this trend is both largely unidirectional and irreversible.

It has been shown that angiosperm vessel elements (in secondary wood) have been phylogenetically derived from scalariform-pitted tracheids by the loss of pit membranes in the regions of tracheid overlap. Therefore, vessel elements which are most tracheid-like, viz., elongate, narrow, many scalariform perforations in the end walls, etc., are the most primitive type. Other known major trends of vessel element specialization (Figs. 3g–k) are: (1) change in perforation plates from scalariform, many barred, and fully bordered, to few barred and borders absent, to more advanced porous oblique and transverse porous plates; (2) angle of end wall highly oblique and tapering (much overlap) to transverse; (3) reduction in vessel element length; (4) change in appearance in transverse section from angular to circular; (5) increase in pore diameter; (6) change in intervascular pitting from scalariform and bordered to opposite and alternate multiseriate; and (7) change in vessel distribution from solitary to extensive aggregate groupings of vessels. Cox (1948a, 1948b) and Adams (1949) used the ratio of average vessel element length to average vessel element diameter as an index of advancement. A relatively primitive condition is expressed by a high ratio, a relatively advanced condition by a low ratio. Concomitant with changes in vessel elements are modifications in the fusiform cells of the vascular cambium from long initials with overlapping ends that divide in a pseudo-transverse manner to advanced initials that are reduced in length, and undergo radio-longitudinal division.

Although the above trends of vessel evolution are believed to be firmly established, Beck (1970) has pointed out the appearance by Middle Devonian time of circular bordered pits in either primary or secondary xylem of coniferophytic progymnosperms and primitive pteridosperms. In his opinion the acceptance of the scalariform bordered pit as primitive in seed plants should be reconsidered. To quote Beck, "In view of the early appearance of the circular bordered pit in the progymnosperms and the preponderant occurrence of this type in the secondary xylem of cycadophytic and coniferophytic gymnosperms, it seems not unreasonable to suggest that the circular bordered pit might be the basic, primitive type in the gymnosperm-angiosperm line of evolution. This is not to say, necessarily, that the circular bordered pits of some angiosperms might not have evolved from the scalariform pits of their ancestors, whether gymnosperm or angiosperm. In these groups this might be interpreted to have been accomplished through neoteny. The circular bordered pits of other groups of angiosperms might simply reflect their ancestry from gymnosperms with circular bordered pits." Furthermore, Baas (1974) and van der Graaff & Baas (1974) have made some very interesting correlations between wood structure and environmental factors. Studies of xylem of 24 dicotyledonous genera, with *Ilex* being the most thoroughly investigated, established that there has occurred a

strong shortening of vessel elements with increasing latitude and altitude. This presumably very important climatic influence on vessel element length (the number of bars per scalariform perforation plate is unaffected) led these workers to the belief that the general phylogenetic trend from long to short vessel elements "must be reversible to a considerable extent" (Baas & van der Graaff, 1974). Their data also suggests that climatic changes have led to other directing influences on wood specialization.

Other well known major phylogenetic trends in the secondary xylem, as revealed by statistically significant correlations using features of vessel elements, include the evolution from tracheids to fiber-tracheids to advanced libriform fibers through a progressive increase in cell length (as compared to vessel elements) with a concomitant reduction in pit size and number and eventual elimination of the tracheid pit border (Figs. 3f–a). Primitive woods have both uniseriate and multiseriate rays that are heterocellular and high-celled; the multiseriate rays have long uniseriate wings (Fig. 2a). Specialization results in the reduction and loss of either the multiseriate or uniseriate rays (or both), the rays becoming homocellular (Fig. 2e) and reduced in height with the uniseriate wings of multiseriate rays reduced to a single cell (Figs. 2b–c). The condition of stratified rays formed by a storied cambium is an extreme advancement. Apotracheal diffuse axial parenchyma is regarded as the primitive state from which more advanced paratracheal types (vasicentric, aliform, confluent) were derived; however, Bailey (1957) points out that the available data do ". . . not provide a thoroughly reliable basis for arranging the diversified patterns in a single linear series of increasing structural specialization." The phylogenetic significance of the absence of wood parenchyma is unclear.

Additional features of wood structure are believed to represent sporadically occurring divergent trends of specialization whose presence in woods does not imply a close genetic relationship. These include helical thickenings on the walls of tracheary elements and fibers, imperforate tracheary elements which become septate or retain a living protoplast, formation of vascular tracheids and vasicentric tracheids, excessive thickening of walls and widening of vessel element diameter (as in lianas), various reticulate perforation plates or other modifications of perforation plates, and extensive aggregations of vessels in diversified patterns (Bailey, 1957). Furthermore, Carlquist (1962) has shown that primitive features of the primary xylem may occasionally be extended into the secondary xylem (paedomorphosis or juvenilism) in plants that are otherwise specialized. This theory of paedomorphosis has recently been challenged by Mabberley (1974).

The great value of wood anatomy as a guide to understanding angiosperm evolution lies not only in the fact that trends toward specialization are well defined, but that all stages in evolutionary specialization are observable in extant angiosperms. Therefore, there is not the slightest doubt that the absence of vessels (Fig. 1a) in eleven genera of woody dicotyledons represents the retention of a primitive feature. The largest number of vesselless genera (7) occur in the Winteraceae, whereas the Trochodendraceae, Tetracentraceae, Amborellaceae,

and Chloranthaceae contain a single vesselless genus each. However, based on the sole evidence of lack of vessels, these genera are not necessarily the most primitive angiosperms, since evolution proceeds independently in all organs and tissues of plants. The absence of vessels in plants belonging to families like Cactaceae is clearly the result of extreme specialization (Bailey, 1966). The importance of how plant habit and the factors of the environment and ecology affect wood structure and the trends of xylem evolution has been emphasized recently by Carlquist (1966, 1969a, 1969b). To date, the single most important guiding principle regarding wood anatomy and phylogeny (Bailey, 1944) emphasizes the impossibility (unlikelihood) that a taxon with specialized xylem gave rise directly to a taxon with less specialzed xylem. Accordingly, wood anatomy is more useful in negations than assertions of positive relationship.

Other features of the secondary xylem are diagnostic in so far as they are restricted to certain families or genera; however, their phylogenetic significance remains dubious. Distinctive tile ray cells are confined to certain genera of the Bombacaceae, Sterculiaceae, and Tiliaceae, whereas upright sheath cells located on the margins of multiseriate rays are of comparatively widespread occurrence. Vestured pits are reported for 24 families of dicotyledons (Bailey, 1933), with a concentration in the Myrtales. Solitary prismatic crystals (Fig. 3m) are relatively widespread, although such forms as raphides (Fig. 3n), druses (Fig. 3l), and crystal sand have a more restricted distribution, and, therefore, are of greater taxonomic interest (Metcalfe & Chalk, 1950).

The relationship of wood anatomy to proposed phylogenetic relationships of the Cronquist and Takhtajan systems of angiosperm classification is presented below, along with examples illustrating the phylogenetic application of wood data at the level of orders within a given subclass, families within an order, and character correlation within a single family. Results presented by Chalk (1937) following an anatomical survey of 1,272 genera of dicotyledons in relation to the general systems of Bentham and Hooker, Engler, and Hutchinson are instructive. Utilizing four degrees of wood specialization—scalariform perforation plates, fiber-tracheids, libriform fibers, and storied structure—Chalk found both primitive and advanced characters widely distributed among Engler's orders. These data indicate that whereas individual families and genera tend to be anatomically homogeneous, orders and categories of higher rank tend to be comparatively anatomically heterogenous (Metcalfe, 1954). It is not surprising, therefore, to find that the Cronquist and Takhtajan subclasses, which are morphologically ill-defined, are also anatomically extremely heterogeneous. The 110 families listed by Metcalfe & Chalk (1950) as containing genera with scalariform perforation plates are widely distributed throughout the subclasses, although scalariform plates occur exclusively in some families and very infrequently in others. Only the Centrospermae (Caryophyllidae), which contains few woody members, tends to be anatomically more or less homogeneous (Metcalfe, 1954).

The subclass Magnoliidae with a preponderance of primitive characters has much to recommend it as the basal group. Although ordinal concepts differ, concentrated within the Magnolialian-Lauralian assemblages are the vesselless Winteraceae and Amborellaceae, as well as the following families whose genera

possess exclusively scalariform perforation plates: Eupomatiaceae, Austrobaileyaceae, Canellaceae, Degeneriaceae, Trimeniaceae, Gomortegaceae, and Illiciaceae (Ranunculidae of Takhtajan). The vesselless species *Sarcandra irvingbaileyi* (Chloranthaceae) is placed in the Piperales by Cronquist and in the Laurales by Takhtajan. Magnolialian families containing vessels with both scalariform and simple perforation plates include Magnoliaceae (simple plates in temperate species only), Himantandraceae, Myristicaceae, Lauraceae, and Monimiaceae. Rather advanced xylem, as evidenced by the occurrence of exclusively simple perforation plates, characterizes Annonaceae, Calycanthaceae, Hernandiaceae (and Gyrocarpaceae), and Lactoridaceae, although in the latter family, the extremely specialized wood is related to growth habit (Carlquist, 1964). Similar habit-related specialized xylem occurs in members of the Schisandraceae. Correlated with the absence of vessels or presence of primitive vessel elements are heterocellular rays, fiber-tracheids, and diffuse or scanty parenchyma.

The diversity of wood anatomy in the Hamamelididae is enormous, ranging from the vesselless Trochodendrales to moderately advanced and advanced families in the Urticales and Leitneriales. The absence of vessels in the Trochodendrales, among other characters, undoubtedly makes this the primitive order. Both Cercidiphyllaceae and Eupteleaceae have vessels with exclusively scalariform perforation plates. Although the Trochodendrales could only have been derived from a vesselless ancestry (from either an extinct or extant group), wood anatomy does not provide positive evidence that the porous genera of the Hamamelididae were derived directly from the Trochodendrales. Along with other wood features, the occurrence of few-barred scalariform perforation plates in a few members of the Ulmaceae, and their corresponding absence in other families, supports the primitive position of the Ulmaceae in the Urticales (Sweitzer, 1971).

Subclasses Dilleniidae and Rosidae are both regarded as derived from the Magnoliidae (within or near the Magnoliales). Wood anatomy is consistent with this conclusion and indicates a derivation from only the most unspecialized members of the magnolialian complex. Although there are no vesselless woods in these two large subclasses, various genera are at a very low level of anatomical advancement. In the Dilleniidae, exceedingly primitive vessel elements (exceeding 2000 μm in length and with over 100 scalariform bars) are found in the Dilleniaceae, Theaceae, and the genus *Saurauia*, with only slightly more advanced elements in other members of the Ericales. In the Rosidae, nearly the total range of variability is present in the basal order Rosales which encompasses the comparatively primitive Eucryphiaceae and Cunoniaceae and the advanced Leguminosae. The need for harmonizing wood anatomy with other systematic evidence is illustrated by the Cornales where wood structure indicates a lower evolutionary level.

As regards the largely herbaceous Asteridae, a high level of xylem evolution is correlated with advanced floral characters. Simple perforation plates predominate, along with other indices of advancement. Members of a few basically herbaceous families (e.g., Campanulaceae, Goodeniaceae) to a limited extent have become secondarily woody in response to highly specific ecological condi-

tions (Carlquist, 1969a, 1969b). Typically, the wood of such plants is unlike that found in fundamentally woody families. Carlquist (1966) describes the wood of Compositae as advanced to highly advanced and notes that it is indistinguishable from woods of other specialized families such as Scrophulariaceae. Because the range of structural variability is so narrow in composites, Carlquist was unable to use major trends of wood evolution for systematic or phylogenetic purposes, but instead had to rely on characters relating to habit, in addition to so-called minor features.

As would be expected, woody anatomy has proven most valuable in intrafamilial classification and phylogeny when families exhibit wide ranges of structural variability. A classic example is found in the Icacinaceae where Bailey & Howard (1941a, 1941b, 1941c) were able to recognize successive levels of evolutionary advancement and utilized anatomical data for subdividing the family into subfamilies and tribes. In the Dilleniaceae I was able to support recognition of two subfamilies and correlate wood data with other vegetative and floral evidence, all of which showed that the Old World genera are, as a whole, more primitive than New World taxa (Dickison, 1967, 1970). Furthermore, the dilleniaceous genus *Acrotrema* is of interest from an evolutionary viewpoint because it is a small, nearly herbaceous plant in an otherwise woody family, and it is one of the few dicotyledonous herbs in which the vessel elements possess exclusively scalariform perforations. The structural variability in the secondary xylem of the Violaceae recently enabled Taylor (1972) to substantiate the division of the subfamily Violoideae into two tribes. Heimsch & Wetmore (1939) found xylem anatomy to correlate to a large degree with inflorescence morphology in evaluating relationships in the Juglandaceae, although attempts to uncover lines of xylem specialization within genera were not successful. On the other hand, when a family is comparatively uniform anatomically, as is the case in the Connaraceae, the significance of xylem data to intrafamilial classification is considerably lessened (Dickison, 1972).

SECONDARY PHLOEM

Unlike xylem, information on the comparative anatomy and evolutionary trends in phloem is meager (Esau et al., 1953). For example, witness the absence of phloem data in Metcalfe & Chalk (1950). The subject of phloem is thoroughly reviewed in Esau (1969). Suggested trends of specialization relate mostly to sieve elements in secondary phloem of dicotyledons and metaphloem elements of monocotyledons, and have by no means been demonstrated to be unidirectional or irreversible. Composing the secondary phloem are the principal conducting cells, the sieve elements, in combination with various amounts of phloem parenchyma, sclerenchyma, and ray parenchyma. With regard to sieve elements, Cheadle & Whitford (1941) recognized two basic types, the sieve cell and sieve tube element. The sieve cell is interpreted as a less specialized element with relatively undifferentiated sieve areas (i.e., narrow pores and thin connecting strands), and lacking highly developed sieve plates and companion cells. More advanced sieve tube elements have specialized sieve plates on the end walls, have accompanying companion cells, and are superimposed on one another in longitudinal series forming a sieve tube. Sieve plates may be compound, that is,

composed of several highly differentiated sieve areas, or simple, that is, composed of a single sieve area. Also, end walls range in orientation from highly oblique to transverse. Although the distinction between these cell types is not always sharp, gymnosperms and lower vascular plants possess sieve cells whereas angiosperms are characterized by sieve tube elements and associated companion cells.

The sieve cell is generally regarded as the primitive type of conducting element from which the sieve tube element arose. Major trends of sieve tube element specialization (Esau et al., 1953) are believed to involve (1) localization of specialized sieve areas on the end walls, (2) change in orientation of end walls from very oblique to transverse, (3) progressive change from compound to simple sieve plates, and (4) progressive decrease in conspicuousness of the sieve areas on the side walls, although the relation between specialization of lateral sieve areas and the sieve tube element is not consistent (Zahur, 1959). Esau (1969) has stressed that comparative data of lateral sieve areas should come only from walls between contiguous sieve elements. The same general trends have also been agreed upon for monocotyledons (Cheadle, 1948; Cheadle & Whitford, 1941). Measurements of cell length, width, and size of sieve pore area have yet to demonstrate the same phylogenetic significance proposed for tracheary tissue. However, Zahur (1959) is of the opinion that there has been a phylogenetic decrease in sieve tube element length (realizing secondary septation can occur) accompanied by decrease in the length of the end walls and increase in the size of sieve plate pores. Following earlier works, Zahur classified sieve tube elements into three categories of increasing specialization: (I) elements long (400 μm or more), with very oblique sieve plates containing 10 or more sieve areas; (II) elements of medium length, with oblique sieve plates containing 2 to 10 sieve areas; and (III) elements short, with slightly oblique to transverse, simple plates. It is clear that there is rather uniform agreement that the most primitive sieve tube elements are ones that most resemble sieve cells.

Zahur (1959) also classified companion cells into types reflecting ascending evolutionary advancement. Type A are cells that are much shorter than the sieve tube elements and occur singly, usually at the corners; type B are cells as long as the sieve tube element; and Type C are cells that are septate in addition to being as long as the sieve tube element. Zahur found companion cell type to be constant within families, and occasionally orders, with the greatest variability occurring in families whose "naturalness" has been questioned.

Although the evidence is indecisive, Zahur (1959) regarded abundant, extremely variable and irregular parenchyma to be advanced, whereas scanty parenchyma showing little variation in size probably represents a primitive condition because of its association with polypetalous families. He could find no basis for deciding whether the presence or absence of phloem sclerenchyma was structurally primitive or advanced. However, Eames (1961) regarded the presence of phloem fibers as an advanced state.

The distribution of sieve element types in the Magnoliales-Laurales correlates with the concentration of other primitive characters. As far as is known, unspecialized sieve cells occur in only one angiosperm, *Austrobaileya scandens*

(Austrobaileyaceae) (Bailey & Swamy, 1949; Srivastava, 1970). It is reassuring that this genus belongs in the otherwise primitive Magnoliidae, although, why the vascular tissues of this genus have remained at a low level of advancement and have not become specialized in response to the liana habit is unclear. Otherwise in the Magnoliales (sensu Cronquist), Type I sieve tube elements occur in Magnoliaceae, Myristicaceae, Canellaceae, Illiciaceae, and Schisandraceae. Type II elements characterize members of Himantandraceae, Monimiaceae, Calycanthaceae, and Lauraceae. Advanced Type III elements distinguish the Annonaceae, a family also with comparatively advanced wood.

Other unrelated families containing Type I sieve tube elements include Cercidiphyllaceae, Passifloraceae, Rosaceae (in part), Myrtaceae, Cunoniaceae, Icacinaceae, Pittosporaceae, Araliaceae, Rutaceae (in part), and Euphorbiaceae. Families containing Type II or III elements include Leguminosae, Elaeocarpaceae, Tiliaceae, Sapindaceae, Meliaceae, Compositae, Moraceae, Urticaceae, Casuarinaceae, Ulmaceae, Garryaceae, Sterculiaceae, and most of the sympetalous families. It should be noted, however, that some dicotyledonous families are very uniform in all genera and species as regards sieve tube element type, whereas other families are quite variable with elements ranging from Type I to Type III occurring in different species. In regard to this extreme variation in sieve element type, Esau (1969) has pointed out that the weakness of this sieve tube element classification lies in the inadequacy of the material surveyed.

Carlquist (1961) noted that there is much variation in the levels of evolutionary advancement in the xylem and phloem within the Compositae. I have encountered a similar lack of correlation in the monotypic urticalean family Barbeyaceae, the single species of which has only simple vessel perforation plates and Type I sieve tube elements (Dickison & Sweitzer, 1970), and in *Saurauia* (Actinidiaceae) which has exceedingly primitive vessel elements with sometimes over a hundred scalariform bars, but Type III sieve elements. Within the Dilleniaceae, *Schumacheria*, the genus with the most primitive wood structure, has very advanced sieve tube elements with simple, transverse sieve plates. It is well known that tissues evolve independently and at different rates. However, the reason for such vast discrepancies in levels of advancement in the vascular tissue needs explanation. Quite clearly, much more comparative information on the phloem needs to be obtained.

PRIMARY VASCULAR SYSTEM

The trends of specialization in the primary xylem of dicotyledons tend to parallel those of the secondary xylem elements (Bailey, 1944), although the trends show an evolutionary lag between both protoxylem and metaxylem, and metaxylem and secondary xylem. All available evidence indicates that vessels arose in woody plants first in the secondary xylem of the stem and then appeared in the metaxylem and protoxylem. Thus, the primary xylem is a reservoir of primitive characters. The presence of vessels in the protoxylem is interpreted as an indication of extreme structural specialization (Bailey, 1944).

As in dicots, the primary xylem vessels of monocotyledons probably originated more than once from scalariformly pitted tracheids (Cheadle, 1953 and

references). However, the phylogenetic sequence is different; vessels in monocotyledons first arose in the late metaxylem of roots, as evidenced from the fact that the most specialized vessel elements always occur in the root metaxylem, and only subsequently extended into the stem and leaf. Within any one organ, vessel element origin and specialization occur first in the late metaxylem and then progressively in the early metaxylem and protoxylem. The distribution of vessel elements in monocotyledonous families shows that they may be restricted within the plant body to the root, to the root and stem, or that they may occur in all parts. Cheadle & Uhl (1948) classified the vascular bundles of monocotyledons into six types based on the appearance of metaxylem elements in transverse section. Utilizing the occurrence of tracheids or the type of vessel-element perforation plate in the late metaxylem as criteria for specialization, they arranged the bundle types in a phylogenetic sequence. However, the fact that vascular bundle type can change rather dramatically in different regions of the same plant casts some doubt on the usefulness of this interpretation.

In the opinion of Bailey (1944) and Cheadle (1953) the independent origins and specializations of vessel elements in monocots and dicots indicate that if the angiosperms are considered to be monophyletic, the monocotyledons must have arisen from a vesselless woody dicotyledon. Cronquist (1968, 1969), however, does not accept the position that vessels evolved independently in monocots and dicots and, therefore, that monocots arose from a primitively vesselless ancestor. In his view, monocots had an aquatic origin (which profoundly influenced their evolutionary history) from dicotyledonous ancestors resembling the modern Nymphaeales. The aquatic habit resulted in the loss of a cambium that resulted in the reduction and loss of vessels. In keeping with this viewpoint, the Alismatidae are considered a near-basal sidebranch of the Liliatae. Kosakai et al. (1970) reported the occurrence of primitive vessel elements in the primary xylem of roots of *Nelumbo* and seriously questioned the idea that monocots were derived from the Nymphaeaceae. These authors emphasized that the Butomaceae and Alismataceae have advanced vessel elements only in the root metaxylem. Accordingly, it is difficult for them to believe, in view of what is known of vessel evolution, that the putatively primitive Alismatidae evolved advanced vessels in an aquatic environment yet gave rise to terrestrial monocots that had more primitive vessel elements in the metaxylem of their roots. The vessel story, according to them, favors the origin of the Alismatidae from terrestrial forms and does not support an aquatic "ranalean" ancestry of the monocotyledons.

Bierhorst & Zamora (1965) following an extensive survey of 1,350 species of angiosperms in 165 families concluded that tracheary elements that mature later in the protoxylem-metaxylem sequence are ontogenetically derived from early maturing protoxylem elements with helical secondary walls by the deposition of additional secondary wall material (second-order framework) in the form of sheets, strands, or both, between the helices (first-order framework) of existing elements. Furthermore, elements in which the second-order framework is deposited synchronously, uniformly, and along the cell edges, are interpreted as primitive, as opposed to advanced elements in which the second-order framework is deposited nonsynchronously and is not restricted to cell edges. The phylo-

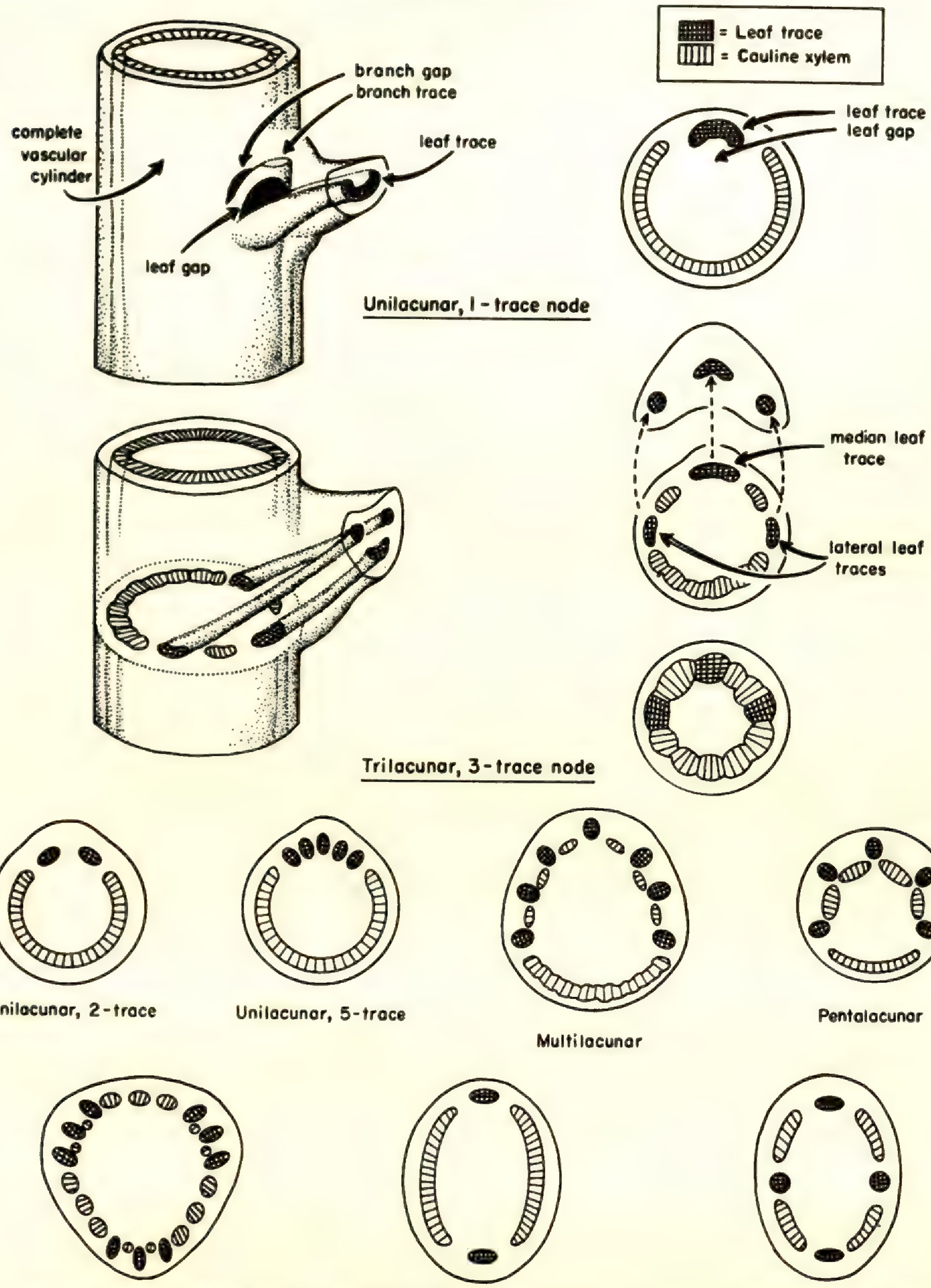

FIGURE 4. Variations in nodal structure in angiosperms. (From A. E. Radford, W. C. Dickison, J. R. Massey & C. R. Bell. Vascular Plant Systematics. Copyright 1974 by Harper & Row, Publ. Used with permission.)

genetic significance of these data, however, is unclear at the present time because the taxonomic distribution of primitive elements includes arborescent monocots (except Agavaceae), most Cyperaceae, Magnoliales, most woody amentiferous plants, Urticales, many woody Rosaceae and Saxifragaceae, and woody members of isolated families that are otherwise herbaceous.

NODAL ANATOMY

The node is that part of the stem to which leaves are attached. Nodal anatomy, accordingly, describes the pattern of vascular continuity between these two organs. Depending upon whether one, three, or five or more leaf gaps (i.e., parenchymatous interruptions) are left in the stele by the departure of vascular bundles (leaf traces) to the leaf, nodes are described as unilacunar, trilacunar, or multilacunar (Fig. 4). The nodal pattern is often expressed in terms of the number of traces and gaps, e.g., a unilacunar node with a single trace would be described as 1:1; a unilacunar node with two diverging traces would be 2 :1; a trilacunar, three-trace node would be 3:3; and so on. The first figure represents the number of traces, the second figure the number of gaps in the vascular system of the stem.

Although most families tend to have a uniform nodal anatomy, some families and even genera have variable nodal structure. Trilacunar nodes occur in the majority of dicotyledons (Sinnott, 1914). Multilacunar nodes are relatively uncommon in dicotyledonous families (Howard, 1970), but are found in members of primitive orders such as Magnoliales, Piperales, and Trochodendrales, and advanced orders such as Umbellales and Asterales. The unilacunar node has an interesting distribution, namely, the Laurales (sensu Takhtajan), Caryophyllales, Ericales, Diapensiales, Ebenales, Primulales, Myrtales, and a majority of the families in the Asteridae. Some orders show transitions in nodal structure, e.g., the Theales from which Schofield (1968) described two possible lines of evolution originating from the ancestral trilacunar condition in the Dilleniaceae. One line maintained the trilacunar node, and eventual amplification culminated in the multilacunar node of the Caryocaraceae. The second line involved reduction to the unilacunar nodes of the Marcgraviaceae and Theaceae.

Since the first comprehensive study of nodal structure and evolution by Sinnott (1914), nodal anatomy has assumed much importance in discussions relating to angiosperm phylogeny. Whether the primitive nodal pattern was trilacunar (Sinnott, 1914), multilacunar (Ozenda, 1949), unilacunar, two-trace (Marsden & Bailey, 1955; Canright, 1955), or trilacunar or multilacunar with two traces diverging from the median gap (Takhtajan, 1969) has yet to be answered. The primary evidence used to support the primitive nature of the 2:1 node are its occurrence (or modifications thereof) in members of the Magnoliidae (Calycanthaceae, Lactoridaceae, Illiciaceae, Amborellaceae, Lauraceae, Chloranthaceae, Monimiaceae, Austrobaileyaceae, Schisandraceae, and Trimeniaceae), the distribution of this type in vascular plants other than angiosperms, and its presence in the cotyledonary node of many dicots even though the mature foliar nodes of the same plants may be tri- or multilacunar (i.e., coyledonary nodes are conservative and thus reflect ancestral conditions).

Recent papers by Conde & Stone (1970) and Stone (1970) have described an amazing diversity of cotyledonary nodal patterns in the Juglandaceae in which nodal evolution appears correlated with functional demands of the seedling. These authors were able to confirm the 2:1 cotyledonary node as primitive in Juglandaceae and suggested the diversification to more complex patterns is functionally related to independent shifts within the family from epigeal to hypogeal seedlings. Furthermore, a suggestion was made that the apparent conservatism of cotyledonary nodes in dicotyledons as a whole may be directly related to the prevalence in many groups of primitive, epigeal germination. Cotyledonary nodal anatomy should, thus, be considered independently of the mature foliar nodes.

Namboodiri & Beck (1968) have recently proposed that the eustele of gymnosperms evolved directly from a protostele by gradual medullation and longitudinal dissection, followed by formation of a cylinder of longitudinal sympodial bundles from which leaf traces diverge radially. In this interpretation the primary vascular system of seed plants is not directly comparable to that of ferns so that the classic filicinean-type leaf gaps may not occur in eusteles. This concept has also been extended to angiosperms (Slade, 1971; Devadas & Beck, 1972). Benzing (1967) concluded that the unilacunar, one-trace or trilacunar, three-trace nodal pattern was probably primitive and agrees with previous workers that the magnolialian families with 2:1 nodes are distinguished by rather advanced floral characters and a presumably derived decussate phyllotaxy.

Howard's (1970) account of nodes with "split-lateral" traces further emphasizes our incomplete knowledge of nodal structure and evolution. Correlating data dealing exclusively with primary vascular systems and studies of nodes in which secondary growth has occurred has yet to be done. Howard (1970) also points out the need for detailed descriptions of nodal vasculature in which the size of bundles, type of bundles, course of bundles, and role of cortical and medullary bundles is taken into account. The entire subject of the stem-node-leaf continuum has been the subject of a recent extensive review by Howard (1974). This paper includes descriptions, methods of study, and discussions of the systematic and evolutionary value of information from this part of the plant body.

LEAVES

Carlquist (1961) has stated that the leaf is "perhaps anatomically the most varied organ of angiosperms, and its anatomical variations often concur closely with generic and specific, occasionally familial, lines." Although anatomical leaf characters are generally useful in the delimitation of taxa, the majority of these characters cannot be readily interpreted ecologically or evolutionally. For example, in the genus *Cratoxylum*, Baas (1970) found the presence or absence of epidermal papillae and a hypodermis able to vary enormously within one subspecies without any evident ecological reason. A few of the characters of leaf anatomy that have proven to be of systematic value and are of potential phylogenetic significance are the following:

Cuticle.—Cuticular features include such characters as distribution and orientation of papillae, striae, and rods.

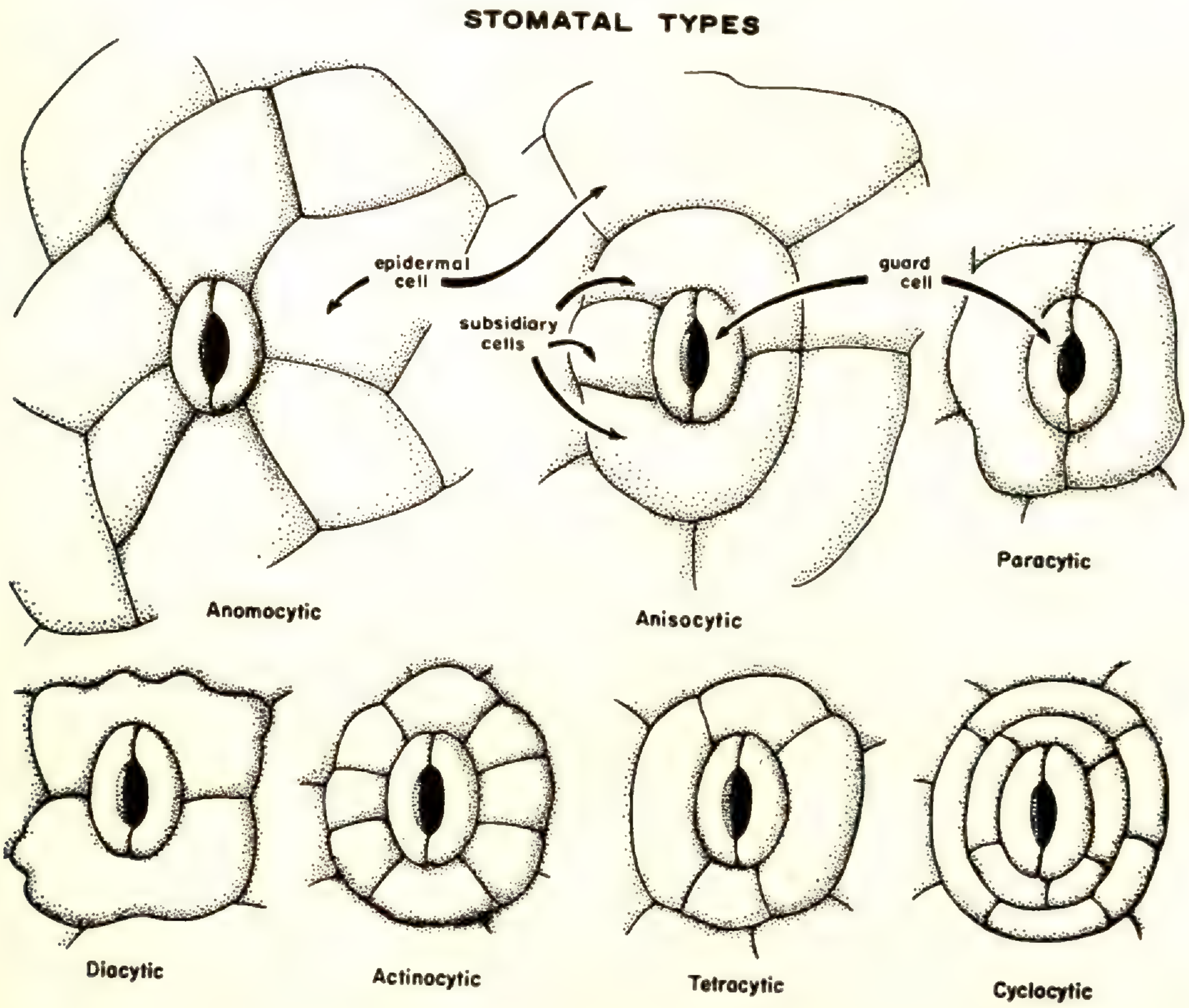

FIGURE 5. Mature stomatal and sclereid types in angiosperms. (From A. E. Radford, W. C. Dickison, J. R. Massey & C. R. Bell. Vascular Plant Systematics. Copyright 1974 by Harper & Row, Publ. Used with permission.)

Epidermis.—Epidermal characters of importance are the presence of a uniseriate or multiseriate epidermis, thickness of walls, and size, shape and contents of cells including the occurrence of papillae and mucilage. Although trichomes have been classically employed for systematic purposes, a classification has yet to be proposed which satisfactorily accounts for their morphological diversity. Metcalfe & Chalk (1950) in commenting upon plant hairs state that "the various types are not always clearly defined, however, and their value for systematic purposes is lessened by the fact that many kinds occur in families which are generally thought to be unrelated, thus making it reasonably certain that the same type of hair must have been evolved along independent lines." Phylogenetic trends in trichomes for angiosperms as a whole have been suggested (see Carlquist, 1961) but they have not had significant influence on phylogenetic thought.

Diversity of stomatal types offers one of the most important and readily observable epidermal characters. Stomatal classification is based, for the most part, on the relationship of subsidiary cells (i.e., epidermal cells associated with a stoma and morphologically distinguishable from the epidermal cells composing the ground mass of the tissue) to remaining epidermal cells and guard cells. The following types of angiosperm stomata are based on their mature appearance (Fig. 5). Definitions follow van Cotthem (1970). (1) Anomocytic (irregular-celled, ranunculaceous type), stoma surrounded by a limited number of cells that are indistinguishable in size, shape, or form from those of the remainder of the epidermis; (2) Anisocytic (unequal-celled, cruciferous type), stoma surrounded by three cells of which one is distinctly smaller than the other two; (3) Paracytic (parallel-celled, rubiaceous type), stoma accompanied on either side by one or more subsidiary cells parallel to the long axis of the pore and guard cells; (4) Diacytic (cross-celled, caryophyllaceous type), stoma enclosed by a pair of subsidiary cells whose common wall is at right angles to the guard cells; (5) Tetracytic, four subsidiary cells are present, two lateral and two terminal; (6) Actinocytic, stoma surrounded by a circle of radially elongated subsidiary cells which form a ring around each stoma; (7) Cyclocytic, stoma surrounded by four or more subsidiary cells which form a ring around each stoma; and (8) Hexacytic, stoma accompanied by six subsidiary cells consisting of two lateral pairs parallel to the long axis of the pore and two polar (terminal) cells; the second lateral pair are as long as the stomatal complex. (This type could be described as a modification of the tetracytic type with an additional pair of lateral subsidiary cells.)

Trends of evolution among stomata types have long been unclear. On the basis of the nearly uniform occurrence of paracytic stomata in the Magnoliales (sensu Takhtajan), Baranova (1972) has recently advocated paracytic types as primitive within the angiosperms. The only taxa in the order lacking this stomatal pattern are *Liriodendron tulipifera* (Magnoliaceae) and *Bubbia perrieri* (Winteraceae), both advanced in their respective families. Correlated with paracytic stoma in the Magnoliales are thickened lamellae on the outer walls of the guard cells and thick-walled epidermal cells with pores in the outer wall, both characters regarded by Baranova (1972) as primitive in angiosperms as a whole. Since it is well known that similar mature stomatal patterns can arise by different developmental path-

ways, an extension of this work utilizing the ontogenetic classification of stomata types by Fryns-Claessens & van Cotthem (1973) would be desirable. It should be noted that paracytic stoma are found in a large number of unrelated and often advanced families. Tomlinson (1974) observes that there are no major groups of monocotyledonous families characterized by a specific type of stomatal development and that speculations regarding the phylogenetic significance of stomatal patterns are premature.

Mesophyll.—Characters of the mesophyll of taxonomic value include the types of mesophyll (bifacial or isolateral) and features of construction, such as relative differentiation into palisade and spongy layers and number of layers in each, distribution and shape of mesophyll cells (isodiametric, stellate, thick-walled), and presence or absence of air-lacunae. The presence or absence of a hypodermis, i.e., a layer or layers of cells beneath the epidermis (either adaxial or abaxial) morphologically distinct from underlying layers, and the number of layers of hypodermal cells are often diagnostic. Also, the presence, absence, and distribution of secretory canals and crystals are frequently of systematic value.

Sclerenchyma.—Leaf sclerenchyma is of two types, sclereids and fibers. A sclereid is a cell varied in form but typically not much elongated, and having thick, lignified secondary walls with many pits. A fiber is an elongated, tapering sclerenchyma cell with a more or less thick secondary wall. Types of sclereids (Fig. 5) based on form include: (1) astrosclereids, branched (ramified) types of sclereid; (2) brachysclereids (stone cells), short, roughly isodiametric sclereids resembling parenchyma cells in shape; (3) filiform sclereids, much elongated and slender, resembling fibers; (4) macrosclereids, somewhat elongated with unevenly distributed secondary walls; (5) osteosclereids, "bone-shaped," with columnar middle part and enlargements at both ends; and (6) trichosclereids, branched, with thin hairlike branches extending into intercellular spaces. Sclereid types based on distribution are (1) diffuse sclereids which are dispersed in the leaf mesophyll, and (2) terminal sclereids which are confined to the ends of small veins. Leaf fibers are termed: (1) girders (a sclerenchymatous connection between a vascular bundle and the epidermis); (2) incomplete (partial) girders (a sclerenchymatous extension from the bundle sheath which does not reach the epidermis); and (3) strands (sclerenchyma free from the vascular bundle sheath and which may be subepidermal). The occurrence and taxonomic usefulness of foliar sclerenchyma in widely diverse families of flowering plants has been well established. Bokhari & Burtt (1970) reported an extraordinarily diverse sclereid composition in the genus *Cyrtandra* (Gesneriaceae) and correlated sclereid morphology with tentative groupings of species made from morphological considerations. Trends of evolution of leaf fiber patterns have been suggested by Ayensu (1973) in the Velloziaceae. In the Magnoliaceae, Tucker (1964) has described apparent phylogenetic trends of specialization among the terminal idioblasts, viz., one toward tracheary cell types, one toward sclerenchymatous terminal cells, and a third toward parenchymatous terminal cells. Since specialized terminal cells are rather widespread in dicotyledons, this character has potentially wider phylogenetic significance.

Venation.—The taxonomic and phylogenetic usefulness of leaf venation pat-

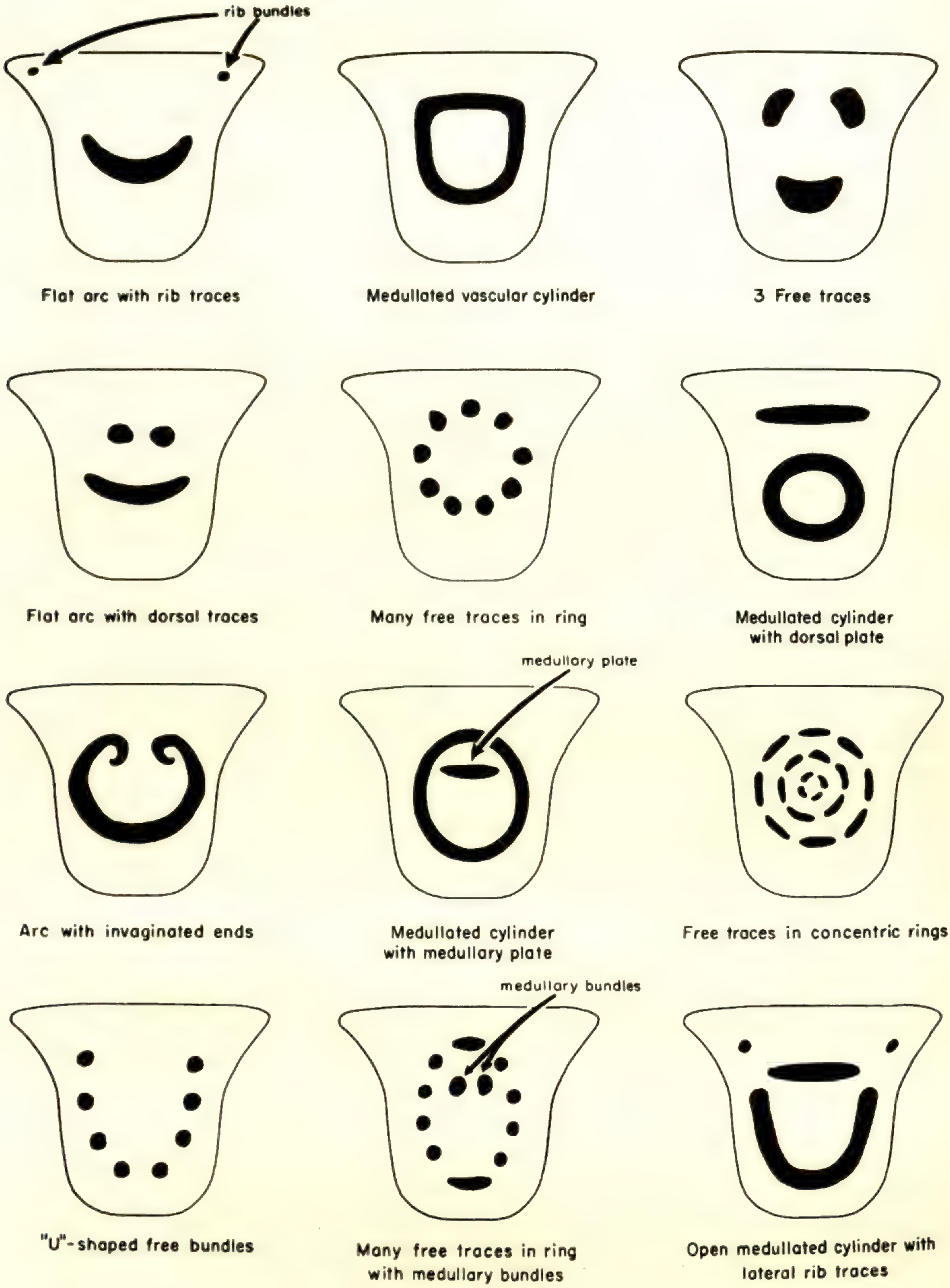

FIGURE 6. Common petiole vascularization patterns in wood dicotyledons. (From A. E. Radford, W. C. Dickison, J. R. Massey & C. R. Bell. Vascular Plant Systematics. Copyright 1974 by Harper & Row, Publ. Used with permission.)

terns has become increasingly apparent in recent years (see Hickey & Wolfe, this symposium). In addition to patterns of major and high order venation, the nature of vein sheathing should also be studied. Sheathing, if present, can be parenchymatous, sclerenchymatous, or a combination of both types to form double sheaths.

The most complete system of classification of major venation patterns in the petiole of woody dicotyledons (Fig. 6) is that of Howard (1962, 1974) although Dr. William L. Stern (personal communication) has questioned the use of stelar terminology in this context. Howard's classification emphasizes the importance of examining sections throughout the length of the petiole to completely understand the changes that occur in the vascular configuration. Accordingly, consideration is given to changes that occur in the vascular system from the time it leaves the stem until it becomes relatively stable in the leaf, e.g., arrangement of the vascular tissue (separate or fused bundles, scattered bundles, medullary bundles, etc.), outline of the vascular tissue (flattened, crescent-shaped, circular, etc.), and location and abundance of sclerenchyma.

Although there is considerable anatomical diversity in petiolar vascularization, trends of evolution in this region of the plant are not readily discernible in angiosperms as a whole. I see little or no obvious correlation between nodal anatomy type and petiole vascularization patterns. Suggested trends of specialization within specific families have been in conflict. For example, within the Dilleniaceae I regarded trilacunar nodes and petioles with unfused bundles more primitive than multilacunar nodes and conditions of fused petiole vascular bundles and the formation of more complex patterns with medullary bundles (Dickison, 1969). These ideas of nodal and petiolar evolution in Dilleniaceae did not agree with the conclusions of Decker (1967) who worked on the Luxemburgieae (Ochnaceae). Within the Luxemburgieae, Decker considered the multilacunar node more primitive than the trilacunar, and petioles with numerous unfused bundles (some of which may be medullary), more primitive than petioles with fused traces and no medullary bundles. In view of the frequent derivation of the Ochnaceae from the Dilleniaceae such contrasting opinions are of interest. Nevertheless, as trends of evolution in laminar venation become clarified and correlated with the petiole in reference to the functional demands of petiole vasculation, then the value of petiole vascularization data for the interpretation of angiosperm phylogeny will increase.

Summary and Conclusions

One of the major contributions of the Cronquist and Takhtajan systems of angiosperm classification was the creation and arrangement of rather large subclasses that reflect major levels of evolution in the angiosperms. Anatomical evidence, in a general way, correlates with evidence elsewhere in the plant to support an arrangement in which the Magnoliidae are the most primitive subclass from which the other angiosperm groups have been derived. The phylogeny of the monocots is much less clear and anatomical studies have yet to provide substantial support to any one idea. Some of the primary contributions anatomy can provide

in the future are to assist in the delimitation of orders and realignment of families and genera, and to help systematically place "anomalous" taxa.

A point stressed in the present paper is that whereas some vegetative anatomical characters can be interpreted as "major trends" of evolution in angiosperms, other anatomical features are only general or diagnostic characters that have no apparent phylogenetic value but may lend support to ideas formulated on other bases. Vegetative anatomical characters whose phylogenetic potential have yet to be fully evaluated and synthesized include aspects of seedling anatomy, origin and anatomy of the periderm, nature of the fundamental tissue and idioblastic cells, and developmental studies of the shoot apex (see Gifford, 1954) and other plant parts. Recent studies on leaf growth and differentiation by Kaplan (1970a, 1970b) have suggested that there is a common pattern of foliar development even among leaves of strikingly different mature form. Evidence of this type has obvious important implications in the solution of problems of plant phylogeny. Because there is a paucity of comparative information on roots, any phylogenetic conclusions based on this organ are premature. With new information being uncovered and correlated with already existing data, new trends of structural evolution in flowering plants are emerging, and trends that were once believed to be well-founded are now being seriously questioned. Clearly, secondary xylem has provided the most useful information toward solving problems of angiosperm phylogeny. This has largely resulted because successful methodologies were employed in studying this tissue. The tremendous wealth of anatomical evidence available in other tissues of the vegetative plant body will likewise become of immeasurable value to phylogeny when techniques are found to provide more meaningful phylogenetic interpretations of these data. For this to be realized, comprehensive anatomical studies need to be carried out utilizing a wide range of materials and approaches that integrate comparative data with development, functional demands of the plant, environmental variation, and the possible adaptive significance of the characters concerned. It may come as a surprise to some to learn that a vast amount of basic descriptive information has yet to be gathered, particularly applying precisely defined terms in current usage. Until a better understanding of the trends of evolution within specific families and genera are attained, there is less hope of uncovering major lines of anatomical specialization within angiosperms as a whole.

The more significant guiding principles of systematic anatomical study as related to angiosperm phylogeny have been eloquently discussed by I. W. Bailey (1951, 1953, 1957). Anatomical characters are no more or less reliable than characters from other parts of the plant. Evolutionary modification of vegetative anatomical characteristics are not necessarily closely synchronized with floral evolution. Since similar anatomical structures have arisen many times in widely divergent taxa, similarites in structural specialization do not necessarily imply close relationship but may be the result of parallel and convergent evolution. As a result, anatomical data have proven most reliable in statements of negation of close relationship rather than positive assertions of relationship. Only when anatomical information is coupled with evidence from other parts of the plant, will a phylogenetic classification of angiosperms be attained.

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THE BASES OF ANGIOSPERM PHYLOGENY: EMBRYOLOGY

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Abstract

Many of the embryological characteristics that may be useful, when employed judiciously and in conjunction with other characters, in arriving at taxonomic conclusions are listed. Several characteristics that show a non-random distribution between families of the Magnoliatae and those of the Liliatae are discussed. Features which are more predominant in the monocotyledons than dicotyledons are: monocotyledonous type of development of the anther wall; amoeboid tapetum; successive cytokinesis of the microspore mother cells to form isobilateral tetrads; helobial endosperm development; and a single cotyledon in the mature embryo. In contrast, those characteristics that are more prevalent among dicot families than monocot families include: basic and dicotyledonous patterns of anther wall formation; simultaneous cytokinesis of microspore mother cells with the formation of tetrahedral tetrads; hemitropous, amphitropous, or circinotropous ovules; ovules with a single integument; an endothelium; *Oenothera, Penaea, Peperomia, Plumbago,* or *Plumbagella* types of megagametophyte development; cellular endosperm; and two cotyledons in the mature embryo. In spite of these differences, those characteristics that are most common—occurring in at least 70%, and usually more, of all angiosperms —are evenly distributed between the two classes and afford a strong embryological unity to the angiosperms. These widespread characters include: four microsporangia per anther; differentiated endothecium; two-celled pollen grains; bitegmic anatropous ovules; *Polygonum* type of megagametophyte development; and nuclear endosperm. Within the two classes distribution of the various characters is not always proportional among the several subclasses and superorders; for example, a unitegmic, tenuinucellate ovule with an endothelium, cellular endosperm with haustoria and Solanad embryogeny predominates in the Ericanae and Asteridae; or helobial endosperm is a distinctive feature of the Alismidae. On the whole, embryological characteristics are remarkably constant at the family level. In those families where variation does occur, genera are usually constant, although a few notable examples of intrageneric, and even intraspecific, variation do exist, as for example, in patterns of megagametophyte development. In addition to the taxonomic usefulness of the grosser aspects of embryology—the major categories of structure or development—some evidence is presented suggesting that variation in details within a single category, such as size, shape, and cellular characteristics of the developing and mature megagametophyte, may be helpful in determining relationships within families, genera, or species.

Since the time of the nineteenth century landmarks in embryological knowledge and the men who made the observations (Amici's discovery of the pollen tube, Hofmeister's recognition of the general structure of the mature megagametophyte and meiosis in microspore mother cells, Strasburger's working out of stages in megagametophyte development and observation of fertilization, and finally the independent recognition that fertilization was double by Nawaschin and Guignard [see Maheshwari, 1950]), many descriptions of various aspects of sexual reproduction (embryology in the broad sense) in a wide variety of angiosperm plants have been published by a host of botanists. During the early part of this century some use was made of embryological characteristics for systematic purposes, for example, Samuelsson's (1913) treatment of the Ericaceae, but it was only with the publication of Schnarf's (1931) *Vergleichende Embryologie der Angiospermen* that impetus was given to this type of synthesis of the accumulating embryological information. Since that time a number of papers, review articles, or books have

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appeared treating one or more embryological characteristics on a comparative basis, frequently relating the observations to one or more taxonomic schemes. This paper is yet another brief attempt in this direction. Throughout, the term "embryology" will be used in the broad sense and is conceived of as incorporating anther, ovule, micro- and megasporogenesis, development of gametophytes, fertilization, and growth of endosperm, embryo, and seed coats.

TECHNIQUES

The early observers, such as Hofmeister, worked almost entirely with fresh and hand-sectioned materials. With the development of paraffin embedding and microtome sectioning, these techniques largely replaced the earlier ones, and the bulk of the observations reported in the literature have been based on thin, stained, serial sections of flowers, ovaries, or ovules. In addition, squashes and smears of anthers have been extensively used, particularly for stages in meiosis and pollen development. In some cases where the megagametophyte, endosperm, or embryo develops highly irregular haustoria which ramify through ovular and/or placental tissues, there has been, during the last 20 years, a return to use of fresh material. Dissections of ovules, combined with microtome sections, have clarified the development and organization of such haustoria (see Chopra & Agarwal, 1958). Dissections have also been used, along with microtome sections, in elucidating embryo development.

The processes of paraffin embedding, microtome sectioning, and staining are relatively tedious. When this is coupled with the facts that such sections are in one plane only, that anthers and ovules may be oriented in a variety of ways even in a single flower (so that "good" sections are often rare and structure must be reconstructed from serial sections), and that for most embryological determinations a closely graded series of developmental stages is needed, it is easy to understand why the number of species for which essentially complete embryological information is available is almost infinitesimal as compared to the total number of angiosperm species. A larger number of species is known with respect to one or a few characteristics, but the total is still very small when compared to the number of angiosperms recognized. This, of course, means that all generalizations based on present knowledge are subject to rejection, modification, or strengthening, as the body of available information increases.

In an attempt to circumvent the tedious aspects of microtome sectioning and the resultant slow accumulation of data for comparative purposes, Herr (1971) has recently developed a technique for clearing and squashing ovules to obtain information on megasporogenesis and megagametogenesis more rapidly. One example of the use of this technique is Smith's (1973) recent study of five species of *Cornus*.

During the past several years embryological materials, particularly pollen, mature megagametophyte, and early embryo, have been prepared for observation with the electron microscope or studied histochemically. These processes are probably even more time-consuming and, to date, with the possible exception of pollen, information is inadequate for use on a broad comparative basis.

Major Reference Works

During the early part of this century, embryological data accumulated rather rapidly and most of the major differences in developmental patterns and structure were recognized. The first text to be based on this extensive information was Schnarf's (1929) *Embryologie der Angiospermen*; this was followed by Maheshwari's (1950) *Introduction to the Embryology of Angiosperms*, and a fair-sized portion of Eames' (1961) *Morphology of the Angiosperms* is devoted to embryology. Maheshwari's text was updated by a series of papers on different embryological topics published, under Maheshwari's (1963b) editorship, as chapters in *Recent Advances in the Embryology of Angiosperms*. The most recent contribution is *The Embryology of Angiosperms* by Bhojwani & Bhatnagar (1974). These books incorporate definitions of terms, descriptions of various developmental patterns and mature structures in all aspects of embryology with their variations, some discussion of possible phylogeny within characters and taxonomic applications of the observed variability, and brief presentations of the physiological and experimental aspects of embryology (which have been less extensively studied than the descriptive ones). Wulff & Maheshwari's (1938) and Maheshwari's (1949) review articles on the male gametophyte of angiosperms are examples of broad treatments of a particular embryological character and there are others of a similar type.

There have been two major attempts to bring together all embryological data on a comparative basis: Schnarf's (1931) book and Davis's (1966) *Systematic Embryology of the Angiosperms*. A Seminar on Comparative Embryology of Angiosperms was held at the University of Delhi in 1967 and, under the editorship of Johri et al. (1967), synopses of the characteristics of 130 families were published. These constitute the major references which deal with all aspects, but books or review articles which sum up individual embryological characteristics on a family basis also occur: Johansen (1950) dealt with embryogeny, Wunderlich (1954, 1959) with tapetum and endosperm, Swamy & Parameswaran (1963) with helobial endosperm, Swamy & Krishnamurthy (1970) with the endothelium in monocotyledons, and Brewbaker (1967) with bi- and trinucleate pollen grains. Souèges, and his students, studied embryogeny in a wide range of species and proposed a classification scheme for embryo development (see Crété, 1963, where much of this work is summarized). A simplification of this classification has been proposed by Mestre (1967) to allow incorporation of species omitted from Souèges's scheme. A third way of classifying embryogeny (Yamazaki, 1974) purports to be more "natural" than those of Johansen and Souèges. Other papers, still more restricted in scope (for example, ones discussing the bisporic or tetrasporic megagametophytes), have been published, but these will not be cited.

Several authors have attempted to show how embryological data may be used for taxonomic purposes, frequently by citing particular genera, tribes, families, or even orders (the examples are in part repetitious from one paper to another): for example, Poddubnaja-Arnoldi (1928), Schnarf (1933), Mauritzon (1939), Maheshwari (1950: chap. 11, 1956, 1961, 1963a), Kapil (1962), Subramanyam (1962), Johri (1963, 1967), Crété (1964), and Bhojwani & Bhatnagar (1974: chap. 13). There have also been listings of those embryological characteristics

that may be useful taxonomically, as for example, those by Schnarf (1933), Maheshwari (1950, 1963a), Cave (1962), Davis (1966), and Bhojwani & Bhatnagar (1974). Just (1946) recommended the use of embryological formulas in the diagnoses of angiosperm taxa much as floral formulas are used.

EMBRYOLOGICAL CHARACTERISTICS WHICH MAY BE USEFUL FOR TAXONOMIC PURPOSES

The following list of characters has been compiled in large part from those previously published lists (see above) and makes no claim to being exhaustive, but the more significant features have been included. It is unlikely that all characteristics are of equal importance. For descriptions, diagrams, drawings, etc. of the various characteristics the reader referred particularly to Maheshwari (1963a, 1963b).

Anther and pollen

Number of microsporangia.

Type of wall development: basic, dicotyledonous, monocotyledonous, reduced.

Endothecium: differentiated or not; number of layers.

Tapetum: glandular or amoeboid; number of nuclei per cell and whether polyploid or not.

Delimitation of microspores: simultaneous or successive; by furrowing or cell-plate formation.

Type of tetrad: tetrahedral, decussate, isobilateral, linear, T, rhomboidal.

Microgametophyte or pollen grain: place of formation of generative cell; number of cells at time of shedding; single or in a cluster, and size of cluster; external morphology such as apertures, exine characteristics, etc. (The latter will be omitted from consideration here and left for the palynologists.)

Ovule

Type: anatropous, orthotropous, campylotropous, hemi(ana)tropous, amphitropous, circinotropous.

Integument(s): one or two; micropyle formed by inner, outer, or both integuments, and if both, straight or zigzag.

Vascular tissue: present or absent; if present, where?

Adjuncts to ovule (pre- or post-fertilization): aril, arillode, caruncle, obturator, etc.

Nucellus: crassi-, pseudocrassi-, or tenuinucellate; nucellar beak? persistent during development? special areas—hypostase, epistase, postament, etc.

Endothelium: present or absent; when present, extent of coverage of megagametophyte.

Megasporogenesis and megagametogenesis

Archesporium: number of cells? divides to form parietal tissue or not.

Type of tetrad: linear, ⊤, ⊥, isobilateral, tetrahedral, coenocytic.

Position of functional megaspore.

Pattern of megasporogenesis and megagametophyte development: *Polygonum*,

Oenothera, Allium, Peperomia, Penaea, Drusa, Fritillaria, Plumbagella, Plumbago, or *Adoxa* type.

Mature megagametophyte: shape; characteristics of synergids and antipodal cells; position and fusion of polar nuclei; type of food reserve, if any.

Haustoria: present or absent; origin and extent.

Fertilization and post-fertilization development

Path of pollen tube: porogamous, chalazogamous, mesogamous.

Endosperm: type of development—nuclear, helobial, cellular and if cellular, orientation of first walls; haustoria—present or absent, origin and extent; persistence in seed; food reserve; ruminate?

Embryogeny: type of development (Johansen, 1950)—Asterad, Onagrad, Chenopodiad, Solanad, Caryophyllad, Piperad; suspensor haustoria present or absent, origin and extent; mature embryo.

Persistence of nucellar tissue in seed.

Source and structure of seed coat.

Apomixis, polyembryony, etc.

Comparative Embryology in the Angiosperms

The facts on which the following comparisons are made are taken primarily from Davis's (1966) book, supplemented by the published synopses from the seminar on comparative embryology at Delhi (Johri et al., 1967) and over 100 individual papers published from 1967 to early 1973.[2] No attempt was made to obtain complete coverage of the pertinent literature for the past 6 to 7 years; only a few journals were checked for embryological articles.

Certain difficulties arise with using Davis's book as the major source of information. There is only indirect evidence of the number of genera and species that have been described in any one family and on which the generalizations are based: the number of papers cited, and, when a family is variable, the number of representatives which may be named. In the seminar synopses no citations are given, so even this type of evidence is missing. Thus, in some families the facts may be based on a single genus or species, while in other families the number of species described has been very much larger. Another and similar problem occurs when a family is described as having two or more variants of a particular characteristic (for example, tetrahedral, decussate, and isobilateral tetrads of microspores or "anatropous to campylotropous" ovules). Often no indication of the relative frequency of the variants is given. Another difficulty is that certain of the characteristics listed as possibly of taxonomic usefulness are not included at all or are mentioned for only a few families. Information may have been lacking in the original papers summarized and/or, faced with the immensity of the task confronting her in compiling the embryological data, Davis may have decided to omit some aspects as probably being of less significance. Whatever the deficiencies of Davis's book, and they are minor compared to the advantages, the task set me

[2] These papers are not cited, but a mimeographed list may be obtained from the author on request.

for this symposium would have been impossible without her extensive compilation of information.

Before starting the factual comparisons, it is probably well to reemphasize that the number of angiosperm species known embryologically, in whole or in part, is very small as compared to the total number of species. Even in one of the more thoroughly studied families, the Asteraceae, Davis (1966) pointed out that, although her bibliography contained over 300 references pertaining to the family, these papers dealt with species in only 15% of the genera and most of the publications were concerned with only one aspect of embryology.

Certain precautions also should be mentioned. In any attempt to arrive at a natural or phylogenetic classification of angiosperms, a single characteristic or single category of characteristics, such as embryology, should not be the sole basis for determining the relationships of a taxon. Although in the following discussion embryological characteristics only are considered, they should be used in conjunction with data from other fields of knowledge, such as those represented in this symposium, in arriving at conclusions. As with other areas, it seems evident that evolution has not proceeded at the same pace in all embryological characteristics, and species may exhibit what is usually considered a basic or primitive variant of a particular characteristic, such as a bitegmic, crassinucellate ovule, along with a derived variant of another, such as a tetrasporic pattern of megagametophyte development. Some variants will have arisen more than once and similarities among species may be the result of parallel or convergent evolution rather than direct relationship. In addition, as pointed out by Davis (1966: 6), "characters are not absolute and their value must be reassessed for each taxon. . . . In other words, the nature of taxonomic characters varies with the taxon."

For several of the embryological characteristics listed earlier, a particular variant is very much more prevalent among angiosperms than the other variants of the same characteristic. There is fairly general agreement that, at least for some of these characteristics, each of the predominant variants represents the basic or more primitive aspect and the other variants are derived. The following constitute these more "primitive" expressions of embryological characters: four microsporangia per anther; two-celled pollen; anatropous, bitegmic, crassinucellate ovule with a multiple archesporium and *Polygonum* type of megagametophyte development; chalazal spore functional; and endothelium absent. There is much less consensus about the phylogenetic status of other characteristics such as the different types of microspore tetrad formation, endosperm development, and embryogeny.

DISTINGUISHING MAGNOLIATAE AND LILIATAE

The distinction between the Magnoliatae and Liliatae is not marked by obvious differences in embryology. Davis (1966: 7) pointed out this embryological unity of the two angiosperm classes in this way: "Hutchinson (1959) recognizes 411 families, of which 342 (83.2%) are dicotyledonous. At the outset, then, there is a dicotyledon to monocotyledon ratio of 5 to 1, so that any character which occurs in five times as many dicotyledonous as compared to monocotyledonous families has an equal frequency in the two groups. . . . it is remarkable that this ratio is almost

always so closely approximated. The fact that this does occur, however, supports the opinion of various authors that there is no embryological distinction between dicotyledons and monocotyledons."

The one most consistent embryological criterion for distinguishing between the Magnoliatae and Liliatae (taxon names throughout are those of Cronquist, 1968 and/or Takhtajan, 1969) is that which led to the original names of the two classes: two or one cotyledons in the mature embryo. This distinction is by no means sharp, however (see Eames, 1961). There are a number of dicotyledons with more than two cotyledons: three occur in most seeds of *Degeneria* as well as in others of the Magnoliales; three commonly are found in *Acer* and *Juglans*; or more than three occur in certain species of *Persoonia* and *Loranthus*. Pseudomonocotyledony occurs more commonly than polycotyledony: either the two cotyledons are of unequal size or one has been lost so that the embryo has a single cotyledon. In such genera as *Trapa* and *Mammillaria* one cotyledon is smaller than the other, while in *Cyclamen* one is well-developed, the other only a small vestige. Two species of *Corydalis* have one normal cotyledon but the second is only a bump opposite it. One species of *Pinguicula* has one normal cotyledon and a second one which stops developing at various stages; two different species have a single cotyledon. *Ranunculus ficaria* is perhaps the best known example of a dicot with a single cotyledon; in this species two cotyledons are initiated and while one most commonly aborts, occasionally both develop. Suppression of one of the two cotyledons is more prevalent in the Apiaceae than any other family: in eight genera the species have one cotyledon while in two other genera some species have two, some one. Aberrant embryos are less common in the monocotyledons, but some genera of the Dioscoreaceae and Commelinaceae have a second cotyledon present in reduced form. *Arum*, *Arisaema*, *Trillium*, and *Paris* have been interpreted as having two cotyledons, one foliaceous (often called the first leaf) and the second a well-developed absorptive organ. Both arise at the same level of the hypocotyl, and their vascular supplies are equal and opposite.

Some other characteristics which are more prevalent in the Magnoliatae or in the Liliatae will be discussed briefly.

1. *Type of Anther Wall Formation.*—The names given by Davis (1966) to two of the four patterns of anther wall development she recognized, dicotyledonous and monocotyledonous, suggest a distinction between the two classes, which, at the present state of our knowledge, does exist. It should be pointed out, however, that information is available for only about 21% of the families and is based, in most cases, only on one or a few species in a family. So far, the basic type has been reported only in dicotyledonous families and, with one possible exception, the same is true of the dicotyledonous type. While the monocotyledonous type is listed as the only type of development in 15 dicot families and as occurring in at least one genus of 7 others, very few monocots are reported to show any other pattern of wall formation.

2. *Tapetum.*—The innermost anther wall layer, supplemented by cells of the connective in contact with the sporogenous tissue, constitutes the tapetum. (Some reports describe the tapetum of certain species as being derived from sporogenous

rather than wall plus connective tissue—see Steffen & Landmann, 1958.) Two basic types are generally recognized—glandular or secretory (which remains cellular and degenerates in situ) and amoeboid (in which the walls break down and the cytoplasm and nuclei migrate among the microspore mother cells)—although Carniel (1963) and Steffen & Landmann (1958) also describe a false periplasmodial tapetum. Those families which show a glandular tapetum exclusively (several families are reported to have both) are 87% dicotyledonous. This is only slightly higher than the normal ratio. An amoeboid tapetum is less common, but 63% of the families in which it is the only type recorded are monocotyledonous; it is the only type found in the Alismidae. The dicot families showing an amoeboid tapetum are scattered from the Magnoliidae to the Asteridae, with more occurring in the superorder Lamianae than elsewhere. Thus, an amoeboid tapetum shows a definite tendency to occur in the monocots rather than the dicots.

3. Cytokinesis and Microspore Tetrad.—The first meiotic division of the microspore mother cell may be accompanied by formation of a wall separating the two nuclei; wall formation again occurs after the second division, and cytokinesis is described as successive. In contrast, wall formation may be delayed until after meiosis II has been completed at which time walls separating the four spores form simultaneously. Again, a few families, both monocot and dicot, are reported to show both patterns of cytokinesis, but the majority are characterized by one or the other. Better than 95% of the families showing simultaneous wall formation are dicots while approximately 92% of those with successive wall formation are monocots. Most of the exceptions occur among the Magnoliidae and Asteridae in the dicots, and the Liliidae among the monocots. Maheshwari (1950) stated that, with a few exceptions, simultaneous cytokinesis is accomplished by furrowing from the periphery and successive cytokinesis by cell-plate formation starting in the center; this cannot be corroborated since the method of division is given for very few families by Davis (1966). Maheshwari (1949) further stated that in dicotyledons the tetrad is usually tetrahedral while in the monocots it is isobilateral. This would suggest a correlation of simultaneous cytokinesis with tetrahedral tetrads and of successive cytokinesis with isobilateral tetrads. Since Davis lists two or more tetrad types for the majority of families, with no indication of the relative frequency of the different forms, this statement and correlation are difficult to check. Those families for which a single type is listed (only 73 out of 214) fit well: 57 dicots to 2 monocots with tetrahedral tetrads, and 2 dicots to 12 monocots with isobilateral tetrads. In addition there is only one family reported to have simultaneous cytokinesis plus only isobilateral tetrads.

4. Number of Cells in Shedding Pollen.—Two-celled pollen as a family characteristic has close to a normal distribution between monocots and dicots, but three-celled pollen is somewhat more prevalent among the Liliatae with 37% of the 47 families showing only three-celled grains being monocotyledonous.

5. Ovule Type.—Of 234 families characterized by a single type of ovule, 197, proportionately distributed among the two angiosperm classes, have an anatropous ovule. Those families having only hemitropous (10) or amphitropous (4) ovules are all dicotyledonous and a circinotropous ovule has not been reported

from any monocot family. Orthotropous ovules are the only ones reported for 18 families, 13 of which are dicots and 5 monocots, while of 5 families having campylotropous ovules 3 are dicots and 2 monocots. Thus hemitropous, amphitropous, and circinotropous ovules might be considered basically dicotyledonous. Hemitropous ovules do occur in certain monocot families, however, in conjunction with other ovular types, primarily anatropous and orthotropous. The only families in which the ovule is so reduced as to be essentially nonexistent as a distinct ovule are dicotyledonous.

6. *Integuments.*—The reduced "ovules" just referred to and those in several genera of another dicot family are ategmic. In 92 dicot but no monocot families the ovules are exclusively unitegmic. Unitegmic ovules do occur among monocots, however, along with bitegmic ones in two families of the Liliidae. Of 210 families in which only bitegmic ovules are found, 59, or close to 30%, are monocotyledonous. Thus, unitegmic and ategmic ovules are a feature found almost entirely in the Magnoliatae. When there are two integuments, the micropyle may be formed by the outer alone, the inner alone, or by both. Families characterized by a micropyle formed by the inner integument are a little more common than those in which it is formed by both (92 to 75) while only two dicot families, both in the Dilleniidae, and not any monocot genera, have micropyles formed by the outer integument alone. About one-third of the families with an inner integument micropyle are monocotyledonous and only about one-sixth of the families with both integuments involved are among the Liliatae.

7. *Endothelium.*—The endothelium is a layer (occasionally more than one) of narrow, radially elongated, more highly cytoplasmic cells which differentiates, concurrently with or subsequent to the degeneration of the nucellus, from all or part of the innermost layer of the integument that is in contact with the megagametophyte. Swamy & Krishnamurthy (1970) discussed the one or more species in 7 different monocot families which had been reported to have an endothelium. They reached the conclusion that in all these cases the layer in question should be interpreted as a temporary stage in development and not as a true endothelium. Davis (1966) apparently largely agrees with this interpretation because she lists only 2 families of monocots as exhibiting an endothelium in contrast to 67 dicot families. Swamy and Krishnamurthy further stated that the families of Magnoliatae with an endothelium are of two types: 18 have crassinucellate, bitegmic ovules later developing nuclear endosperm, while the majority (about 50) possess tenuinucellate, unitegmic ovules and later produce cellular endosperm. They indicated that they would discuss the 18 families in a later publication, but the implication was that these, like the monocots, do not produce a typical endothelium. If their interpretation can be accepted, endothelial development is limited to a comparatively small group of relatively advanced dicotyledonous families. Even if the interpretation is not accepted, an endothelium is primarily a feature of ovules of dicot families in the Dilleniidae, Rosidae, and Asteridae.

8. *Ovule Archesporium.*—The hypodermal cell (or cells) at the tip of the young nucellus which gives rise to the megaspore mother cell(s) constitutes the archesporium. There may be one cell, two, or several. While a unicellular archesporium is proportionately distributed among the families of the two angio-

sperm classes, a multicellular condition is not: it is regular in 43 and frequent in 23 dicot families in contrast to regular in 2 and occasional in 1 monocot families.

9. Megagametophyte Development.—The patterns of development from megaspore mother cell to mature megagametophyte are based on the number of spores that take part in the development, the number of mitotic divisions after the two meiotic ones, the total number of nuclei at the completion of divisions, and the cellular organization of the mature gametophyte. The *Polygonum* type (monosporic; 3 mitoses; 8 nuclei; and 2 synergids, 1 egg, 2 polar nuclei, and 3 antipodal cells) is by far the most common, occurring exclusively in close to 80% of the families and distributed equally between the Liliatae and Magnoliatae. The other patterns of development are much less frequent and only in 11 families, 8 of them dicot, is one of them the only developmental type exhibited. Certain of these other types, namely *Oenothera* (monosporic; 2 mitoses; 4 nuclei; and 2 synergids, 1 egg, and 1 polar nucleus), *Penaea* (tetrasporic; 2 mitoses; 16 nuclei; 2 synergids, 1 egg, 4 polar nuclei, and 3 groups of 3 "antipodals"), *Peperomia* (tetrasporic; 2 mitoses; 16 nuclei; and 2(1) synergids, 1 egg, 7(8) polar nuclei, and 6 scattered antipodals), *Plumbago* (tetrasporic; 1 mitosis; 8 nuclei; and 1 egg, 4 polar nuclei, and 3 widely separated "antipodal" cells), and *Plumbagella* (tetrasporic; 1 mitosis; 4 nuclei; and 1 egg ($1n$), 2 polar nuclei ($1n$ and $3n$), and 1 antipodal cell ($3n$)), have to date not been reported in any monocotyledonous species. The other four types, *Allium* (bisporic; 2 mitoses; 8 nuclei; and 2 synergids, 1 egg, 2 polar nuclei, and 3 antipodal cells), *Drusa* (tetrasporic; 2 mitoses; 16 nuclei; and 2 synergids, 1 egg, 2 polar nuclei, and 11 antipodal cells), *Fritillaria* (tetrasporic; 2 mitoses; 8 nuclei; and 2 synergids ($1n$), 1 egg ($1n$), 2 polar nuclei ($1n$ and $3n$), and 3 antipodal cells ($3n$)), and *Adoxa* (tetrasporic; 1 mitosis; 8 nuclei; and 2 synergids, 1 egg, 2 polar nuclei, and 3 antipodal cells), occur in both classes, the *Allium* type being the more common in both.

10. Pollen Tube Entry.—In the vast majority of angiosperms the pollen tube enters the ovule porogamously, that is, via the micropyle. In five dicot families pollen tube penetration is chalazogamous; it enters the chalazal end of the ovule and follows a course along the lateral surface of the megagametophyte until it reaches the micropylar end where it enters the gametophyte itself in the usual fashion. One dicot family is mesogamous, with the pollen tube initially penetrating the ovule at some side point before making its way to the micropylar end of the gametophyte. No monocotyledonous genera have been reported to show either chalazogamy or mesogamy.

11. Endosperm.—Nuclear endosperm development results when division of the primary endosperm nucleus—the product of fertilization of the polar nuclei—and of subsequent nuclei is not followed by wall formation leading to a coenocytic condition. The number of free nuclei formed varies from relatively few to well in the hundreds before wall formation starts, but in most species, though not all, the endosperm does become cellular—usually completely but sometimes only in part. In direct contrast to the nuclear is the cellular type of endosperm development in which nuclear divisions are accompanied by wall formation (most commonly throughout development, but at least during the early stages) and the endosperm is cellular from the beginning, not just in later stages. In helobial

endosperm development division of the primary endosperm nucleus is followed by wall formation, but the two cells formed are normally of very different sizes—the micropylar large and the chalazal small. Subsequent development in the micropylar chamber corresponds to the nuclear pattern—at first coenocytic, then becoming cellular. In the chalazal chamber the nucleus may remain undivided or undergo a few to several divisions, but the portion of the endosperm which it forms always remains much smaller than that formed by the micropylar chamber. Reports of helobial endosperm describe the chalazal chamber as being free nuclear in some families, cellular in others. Because of its small size it is quite possible that the chalazal chamber has been overlooked in some cases, or interpreted as a persistent antipodal cell, and since the behavior of the micropylar chamber is nuclear, endosperm development may have been mistakenly classed as nuclear in these cases. Of these patterns nuclear development occurs in the largest number of families, helobial in the fewest. Nuclear development shows a proportionate distribution between Liliatae and Magnoliatae, but cellular and helobial do not. Of 82 families showing only cellular endosperm, 80 are dicotyledonous and among 6 "mixed" monocot families only 1 is reported to have any species exhibiting cellular development. Helobial endosperm shows the opposite distribution: of 17 families in which the endosperm is exclusively helobial, 15 are monocotyledonous and of the 21 "mixed" dicot families only 6 are reported to show some species with helobial endosperm. Swamy & Parameswaran (1963) have reviewed the occurrence and characteristics of the helobial pattern of development. They discussed endosperm development in many dicot genera, particularly among 12 genera in the tribe Saxifraginae. They point out three distinguishing characteristics between helobial endosperm as it occurs in monocots and that reported in dicots. (a). In monocots division of the primary endosperm nucleus occurs close to the antipodal cells and the chalazal chamber is always much smaller than the micropylar, while in dicots the position of the division is variable and the chalazal chamber is not always smaller than the micropylar. (b). Initial divisions in the micropylar chamber are free-nuclear in both dicots and monocots but cell formation, if it occurs, takes place before the chalazal chamber becomes cellular in monocots and after it is cellular in dicots. (c). Any divisions that occur in the chalazal chamber are nuclear in monocots and cell formation, if it occurs at all, succeeds that in the micropylar chamber. In dicots cell formation in the chalazal chamber occurs at the first and subsequent divisions in a number of genera. In others, although the initial divisions are nuclear, cell formation in the chalazal chamber precedes that in the micropylar chamber. Swamy & Parameswaran (1963: 48) concluded that "the presumed cases of helobial endosperm in dicotyledons represent, in each case, a modified aberrant ontogeny of the general condition (cellular or nuclear) occurring in the respective families. Therefore, such ontogenies in the dicotyledons are totally removed ontogenetically and phylogenetically from the true helobial ontogeny of the monocotyledons." If one accepts their interpretation, the "true" helobial endosperm becomes even more a distinctive characteristic of the Liliatae. Micropylar, chalazal, and/or lateral portions of the endosperm may grow out to varying sizes and shapes and invade integument(s), funiculus, placenta, etc. where they apparently serve an haustorial

function. Haustoria (ignoring variations in position and structure) may be associated with nuclear endosperm but are much more common with cellular endosperm, and the chalazal chamber of helobial endosperm is frequently haustorial. Because of the prevalence of haustoria in association with cellular endosperm and of this type of endosperm in dicots as compared to monocots, endosperm haustoria are more common in dicots. This difference in distribution of haustoria is offset to some extent by the greater frequency of helobial endosperm, and its associated chalazal haustorium, in monocots. Crété (1951) has enlarged on the distribution and phylogenetic interest of endosperm haustoria in angiosperms, particularly in the sympetalous dicotyledons. Eames (1961) stated that endosperm persists in the seed of more monocots than dicots, but data were not presented in Davis's (1966) summary of characteristics to allow confirmation of this statement.

12. Embryogeny.—The earlier two of the three systems of classification of embryo development—Johansen's (1950) and Souèges's (see Crété, 1963)—are based on the same criteria: first on the plane(s) of division during the first few cell generations and then on the relative contribution to the mature embryo of the individual cells of the proembryo, while in Yamazaki's (1974) classification emphasis is primarily on the latter aspect. Souèges's scheme is the more detailed of the three and a larger number of general types is recognized. To classify a particular species according to this scheme, a high degree of accuracy is needed in following the cell-by-cell development of the proembryo, more than is usually given in most descriptions. Johansen's system, while requiring careful observation particularly at certain critical stages, permits a classification as to type of development for most embryos described in the literature, and it is this system which Davis (1966) employed in her compilation. Yamazaki's key to embryogenic types had not been published at the time Davis was preparing her book, but I doubt that she would have used it in preference to Johansen's. Considering only the six basic types of development and none of the variations (which Johansen recognized within all but one type), embryogeny in 166 families follows a single pattern of development while in 105 two or more patterns are reported. Distribution between monocots and dicots is not the same for the several patterns: Piperad and Solanad types have not been reported in any monocot, not even in the "mixed" families, and most of the other types do not show the 5 dicot to 1 monocot segregation expected if distribution were proportionate between the two classes. The Chenopodiad type is characteristic of 5 dicot and 1 monocot families but the others diverge more or less from this: Onagrad type 40 to 4, Asterad type 41 to 10, and Caryophyllad type 12 to 13. The "mixed" families show a similar distribution of embryogenic types, except for the Caryophyllad type which has been reported to occur in at least one genus of 16 dicot families as compared to 3 monocot families.

Thus, if one looks carefully, it is possible to find uneven distribution between the Liliatae and Magnoliatae of several embryological characteristics, but this does not mean that it would be easy to classify an unknown species to one class or the other on the basis of embryology alone. In the characters that vary between the two, except for the number of cotyledons, the unevenness is expressed in one of two ways. (a). A shift occurs in the relative frequency of occurrence, by

family, of that characteristic up or down from the approximate 5 to 1 ratio that would be expected if the characteristic were equally distributed among the families of the two classes (5 dicot families to 1 monocot family). When the shift in frequency of occurrence of a characteristic is toward the dicotyledons, there is an exaggeration of the difference in number of dicot and monocot families showing the character, but this may not be readily apparent without an overall comparison of the type just made. When the shift is in the opposite direction, toward the monocotyledons, the difference also is not readily apparent. Because of the considerably larger number of dicot families, even if the ratio shifts from 5:1 to 2:1, there will still be more dicot than monocot families exhibiting the characteristic. Examples of divergence from the expected frequency are seen in the distribution of tapetal types, bitegmic ovules, three-celled pollen grains, etc. (b). When the difference in distribution is much more clearly expressed, as when a particular characteristic occurs exclusively, or almost exclusively, in either the monocots or the dicots, that character almost always is one which occurs in a relatively small proportion of angiosperm families or genera. Some examples are certain of the types of megagametophyte development (*Penaea*, *Peperomia*, *Oenothera*, etc.), helobial endosperm, Piperad or Solanad embryogeny, and chalazogamous pollen tube penetration. The most common structures or patterns of development, such as *Polygonum* megagametophyte development, bitegmic anatropous ovule, nuclear endosperm, anthers with four microsporangia and a differentiated endothecium, are evenly distributed in the two classes resulting in the considerable embryological homogeneity that characterizes the angiosperms.

DISTINGUISHING HIGHER LEVEL TAXA WITHIN THE MAGNOLIATAE AND LILIATAE

Having seen to what use embryological characters can be put in attempting to distinguish between the two classes of angiosperms, the question remains as to whether such characteristics may be more or less useful as distinguishing features among taxa at various lower levels of the taxonomic hierarchy. Because there are so many embryological features which show variation and because this report makes no pretense at being an exhaustive survey of the subject, it has been necessary to select only some of these characters for discussion. Some aspects already considered with respect to dicots versus monocots will be omitted from further discussion; others will be touched on again but from another point of view.

The number of cells, often seen only as nuclei, in the pollen grains at the time they are shed from the anther may be two or three, as already pointed out. Distribution of families showing two-celled, three-celled, or both types of grains by subclass gives no clearcut distinctions, but families with two-celled grains or both two- and three-celled ones predominate in the Magnoliidae, Ranunculidae, Hamamelididae, Dilleniidae, Liliidae, and Arecidae, while three-celled, or two- plus three-celled, families are most common in the Caryophyllidae, Alismidae, and Commelinidae. A much more detailed analysis of this pollen characteristic has been made by Brewbaker (1967), who presented data for 1908 species from 1219 genera in 265 families. Of these families 179 were entirely binucleate, 54 entirely trinucleate, and 32 both bi- and trinucleate. Many of the largest families,

such as the composites, orchids, and grasses, had a single pollen type. He found that "with almost surprising regularity binucleate and trinucleate pollen types are mutually exclusive in angiosperm species and genera. Only 10 genera studied include both binucleate and trinucleate species." Of these 10 genera Brewbaker accepted only 5 as convincingly containing both types of pollen. He arranged the families and the information he had compiled on two family trees, the one for the dicots following Takhtajan (1954) and that for the monocots following Hutchinson (1959). It is recommended that the reader study these informative diagrams in the original paper (Brewbaker, 1967). With the aid of these he was able to draw a number of conclusions about the occurrence of trinucleate pollen. (a). Aquatic taxa with submersed flowers normally have trinucleate pollen (3 genera are exceptions), but this does not apply to emersed flowers of subaquatic or marsh plants. (b). "Trinucleate taxa regularly trace back to binucleate taxa, while the reverse need not be postulated in a single instance. Schüroff's (1926) proposal that trinucleate pollen is a phylogenetically advanced trait appears wholly validated." (Brewbaker, 1967: 1071). (c). Trinucleate pollen has arisen independently many times during angiosperm evolution. In the line of evolution through the Rosales trinucleate pollen appeared many times; for example, there are six "mixed" families in the Gentianales alone. In contrast to this the other major evolutionary lines show a less frequent appearance of the trinucleate condition: once in the Hamamelidales line, once in the Ranales, five in the Theales, and at no more than six sites in the monocotyledons. A number of these sites of origin are related to the evolution of aquatic taxa. (d). "We must conclude that the earliest angiosperms were endowed with a unique binucleate pollen grain, distinguishing them from more primitive taxa." (Brewbaker, 1967: 1082).

The Caryophyllidae is the only subclass of angiosperms in which no family has exclusively anatropous ovules though they do occur in some families in conjunction with other types. The predominant types are the curved ones—campylotropous and amphitropous—alone or in conjunction with others. The larger subclasses Dilleniidae, Rosidae, Asteridae, and Liliidae show predominantly anatropous ovules and this is also true of the smaller Ranunculidae, Alismidae and Arecidae. Of 18 families in which the ovules are exclusively orthotropous, 6 are in the Magnoliidae (Chloranthaceae, Piperaceae, Saururaceae, Rafflesiaceae, Hydnoraceae, Ceratophyllaceae), 3 in the Hamamelididae, and 4 in the Commelinidae. The basic type of ovule would appear to be the anatropous; it occurs in the Magnoliales, Ranunculales and Alismales, and is found in all "central" orders as well as being characteristic of such advanced families as the Asteraceae and Orchidaceae. The other types have probably arisen independently several times and the occurrence of, for example, an orthotropous ovule in two families is not a good indication that these families are related.

As pointed out earlier, unitegmic ovules are almost exclusively a feature of dicotyledons. In general the number of integuments is a family characteristic: of 281 dicotyledonous families only 19 have both unitegmic and bitegmic ovules. The unitegmic condition is thought to be derived from the bitegmic either by fusion of the two or by loss of one; ovules showing intermediate steps in both fusion and loss have been described. The distribution of the two types of ovules

among the dicots also indicates that the unitegmic condition is derived. Two integuments are predominant in the Magnoliidae, Ranunculidae, and Caryophyllidae; the proportion of families having a single integument increases slightly in the Hamamelididae and Dilleniidae (here they all occur in one superorder, the Ericanae), while in the Rosidae, families with unitegmic ovules outnumber those with bitegmic ones about 3 to 1, and the Asteridae are almost exclusively unitegmic.

In addition to number of integuments, their thickness in cell layers, commonly at the mature ovule stage, has often been recorded, but one aspect which is rarely described in research papers and has not been covered by Davis (1966) at all is their ontogeny. Bouman (1971) and de Boer & Bouman (1972) have expressed the opinion that characters of seed coats (mature integuments) may be of doubtful taxonomic significance unless accompanied by observations of development, since apparently-similar multilayered integuments may have arisen differently during development. They also suggested that "histogenesis of the integuments must be taken into account in discussions concerning the homology of integuments" (de Boer & Bouman 1972: 627).

The extent of the nucellus beyond the megaspore mother cell has been described for over 300 families. As pointed out earlier, it may be composed of a single layer of cells, and the ovule be tenuinucellate, or there may be one to several layers of cells between the outer layer and the sporogenous tissue. These layers may have been derived from the parietal cell(s) formed by division of the archesporial cell(s) (crassinucellate ovule), by division of the epidermal layer (may be differentiated from the parietal type and called pseudocrassinucellate), or by both. In a little less than two-thirds of the families described all ovules are crassinucellate; a number show some genera crassinucellate and others tenuinucellate. No families characterized by tenuinucellate ovules are found in the Hamamelididae, Caryophyllidae, or Arecidae and only a few occur in the Magnoliidae and Ranunculidae (Rafflesiaceae, Hydnoraceae, Sarraceniaceae, Circaeastraceae, and most of the Podophyllaceae). The Rosidae families are 3 to 1 crassinucellate but the tenuinucellate families occur primarily in the superorders Rosanae and Celastranae; similarly the Dilleniidae are 2 to 1 crassinucellate but again almost all the tenuinucellate families are in one superorder, the Ericanae. Families of the Alismidae and Liliidae are also about 2 to 1 crassinucellate while those of the Commelinidae are about equally divided between crassi- and tenuinucellate. The Asteridae are almost completely tenuinucellate with only some genera of the Convolvulaceae and the *Ehretia* section of the Boraginaceae forming parietal tissue, while the Asclepiadaceae and a rare species in the Lamiaceae show divisions in the nucellus.

Young & Watson (1970), in a computational analysis of 543 genera based on 83 attributes, many of which were embryological, arranged the dicot families considered in two main groups, "Crassinucelli" and "Tenuinucelli," thus emphasizing the possible significance of variation in this ovular character among the angiosperms. Their treatment of families corresponds only in part with the orders and superorders of Cronquist (1968) and Takhtajan (1969).

The amount of tissue built up in crassinucellate ovules varies from very little to considerable. Ovules with thick nucelli are found primarily in the Magnoliidae, the superorders Dillenianae and Malvanae of the Dilleniidae, in about half the families of the Hamamelididae, and in several families of the Rosidae, particularly in the superorder Rutanae. All nucelli in crassinucellate monocots tend to be moderately-thin to thin. Although this is rarely stated in Davis's (1966) synopsis of a family, in the Ericanae and Asteridae the single nucellar layer normally degenerates completely between the tetrad and mature megagametophyte stages so that the latter is in contact with the inner layer of the integument. It is mostly these families that show Swamy & Krishnamurthy's (1970) "true" endothelium.

A comparison of the distribution of unitegmic ovules, the tenuinucellate condition, and an endothelium shows that they frequently, though not invariably, occur together. As stated earlier, unitegmic, tenuinucellate ovules with an endothelium are concentrated in the Asteridae and Ericanae, and are found also in another group of families occurring in the Aralianae of the Rosidae (here some families have ovules with one or occasionally two parietal layers although the Apiaceae are strictly tenuinucellate). This distribution suggests that the tendency to one integument, no build-up of nucellus, and differentiation of an endothelium must have been expressed in two different major evolutionary lines of the dicotyledons, as proposed by Cronquist (1968) and Takhtajan (1969), one through the Rosales to the Scrophulariales, Polemoniales, Lamiales, Asterales, etc. of the Asteridae and to the Aralianae of the Rosidae and the other through the Theales to the Ericanae.

Two integuments so commonly go hand-in-hand with the crassinucellate condition and one integument with the tenuinucellate condition that Philipson (1974) recently advocated that considerably greater emphasis be placed on these aspects of the ovule in determining relationships, and in proposing major phyletic lines, within the dicotyledons. He discussed the distribution of the two characteristics, particularly the exceptions to two integuments occurring with the thick, and one with the thin, nucellus, and attempted to distinguish between what he called "the sporadic independent acquisition of the characters and their consistent presence in major evolutionary lines" (Philipson, 1974: 90). This recommendation would involve removal of the families of the ericalean complex from the Dilleniidae and their alliance with the other sympetalous families of the Asteridae and thus recognize a single major evolutionary line for the sympetalous dicotyledons.

It has already been suggested that the crassinucellate, bitegmic ovule is the primitive one. Support for this conclusion has been supplied by Sporne (1969), who found several highly significant correlations between the crassinucellate condition or the occurrence of two integuments and other dicotyledonous characters, both floral and vegetative, which are correlated and considered to be primitive.

Although 10 different patterns of megagametophyte development are generally accepted and others have been suggested, only one—the *Polygonum* type—is at all common. Maheshwari, in 1950, stated that it occurred in at least 70% of the angiosperms then known. At the present state of knowledge, the *Polygonum* type is the only type of development reported for almost 80% of the families where

development has been described (294). Only 11 families are characterized by a different single type of development. In the 56 families showing two or more patterns of development, the *Polygonum* type usually predominates: of the 20 different combinations of types which have been reported to occur in any family, the *Polygonum* type occurs in 16 and is apparently the predominant type in at least 9 of these combinations. Although, from the compiled data, there is no clear information about the total numbers of species involved, the family figures suggest rather strongly that the *Polygonum* type of development is even more prevalent than Maheshwari's 70% or the 80% of the families would indicate. It predominates in all subclasses of the angiosperms with the Rosidae containing more families either with a single different type of development (5 families and 5 different types of development) or a combination of types (16 families). Of the variant patterns of development, the *Allium* type is most frequent, characterizing 6 families and occurring with the *Polygonum* type in 29 families and as one of the types in 10 other combinations. It is an uncommon type in the Magnoliidae and Ranunculidae. The other variants are more restricted in distribution. The *Oenothera* type characterizes the Onagraceae (Rosidae) and apparently does not occur elsewhere. The *Drusa* type, in a reduced version, occurs in all Limnanthaceae (Rosidae) and is found usually in only 1 or 2 species in 7, possibly 9, other families scattered from the Hamamelididae to the Liliidae (Ulmaceae, Euphorbiaceae, Tamaricaceae, Apiaceae, Scrophulariaceae, Asteraceae, and Liliaceae). *Penaea* type development, as would be expected from its name, characterizes the Penaeaceae (Rosidae) and is found elsewhere in some Combretaceae and Malpighiaceae, one species of Apiaceae (all Rosidae), questionably in one species of the Plumbaginaceae (Caryophyllidae) and in a few Euphorbiaceae (Dilleniidae). Development of the *Peperomia* type characterizes the Gunneraceae (Rosidae), has been reported to occur in modified form in one species of Berberidaceae (Ranunculidae), is typical of *Peperomia* of the Piperaceae (Magnoliidae), is found in two species of Rubiaceae and possibly in some Asteraceae (listed in the Delhi seminar synopsis but not Davis) (Asteridae), and is reported for one species of the Euphorbiaceae (Dilleniidae). The *Adoxa* type characterizes the Adoxaceae (Asteridae) and elsewhere has been found to occur occasionally in one genus of Hydnoraceae (Magnoliidae), in some ovules of the Ulmaceae (Hamamelididae), in one species of the Aizoaceae and occasionally in two genera of Plumbaginaceae (Caryophyllidae), in one species of the Euphorbiaceae (Dilleniidae), in two species of Solanaceae, the genus *Sambucus* of the Caprifoliaceae, and one species of Asteraceae (Asteridae), in four genera of Liliaceae, one species of Trilliaceae and of Zingiberaceae, and occasionally in some Orchidaceae (Liliidae), and in one species of Commelinaceae and five of the Poaceae (Commelinidae). None of the other three variants—*Fritillaria*, *Plumbago* and *Plumbagella*—is characteristic of an entire family. The latter two occur only in the Plumbaginaceae, the *Plumbago* type in two genera and the *Plumbagella* type in one. The *Fritillaria* type of development, which more people have probably seen than any other (even the *Polygonum* type), since it occurs in *Lilium* and *Fritillaria*, the only genera for which slides showing megagametophyte development are sold commercially, occurs in a wider range of

families: in two genera of the Piperaceae (Magnoliidae), two genera of the Plumbaginaceae (Caryophyllidae), irregularly in one species and occasionally in others of the Tamaricaceae and in one species of the Euphorbiaceae (Dilleniidae), in one species of Cornaceae (Rosidae), in some of the Asteraceae (Asteridae), and in five genera of the Liliaceae (Liliidae).

While a single type of megagametophyte development occurs in the majority of families, there are, as has just been pointed out, a number of families in which more than one type has been found. Mixed families occur in all subclasses of angiosperms but are less frequent in the Magnoliidae, Ranunculidae, Hamamelididae and Alismidae, and more common in the Asteridae and Liliidae. In the mixed families a particular type of development often characterizes a genus, but there are a number of examples where different species of a single genus develop via different pathways, and variation also may occur within a single species, even within the same inflorescence or the same individual. Variation within species has been reviewed by Hjelmqvist (1964). The families showing the greatest intrafamilial variation are the Euphorbiaceae, Plumbaginaceae, Asteraceae, and Liliaceae, all showing five or six different types of development.

The commonly held opinion is that the monosporic 8-nucleate gametophyte (*Polygonum* type) is the most primitive. As pointed out by Maheshwari (1950), it is rather easy to conceive of all variants being derived from the *Polygonum* type by failure of walls to form after meiosis II or after both meiosis I and II and by a reduction in the number of mitoses. A change in the reverse direction—from any of the different types to the *Polygonum* type—is much more difficult to envision. Such a change would involve an addition of walls (as in the tetrad) and an increase in number of mitoses (no variant has more than two mitoses while the *Polygonum* type has three), and the general tendency throughout the vascular plants has been toward a reduction in the gametophyte, not an increase. Within many of the types of angiosperm megagametophyte development, there has been additional evidence of reduction in mitoses. While the nucleus at the micropylar end of the developing megagametophyte always completes all divisions, one or more of those toward the chalazal end may not divide. In certain basically bisporic and tetrasporic megagametophytes this failure of divisions at the chalazal end has gone so far as to make the gametophyte pseudomonosporic, as in the Podostemaceae (*Allium* type), Limnanthaceae (*Drusa* type), and three species of Asteraceae (*Drusa* type). Anyone who has looked at a number of examples of the final stages of megagametophyte development in lily may well have seen an example of this reduction in mitoses. The chalazal-most nucleus of the 4-nucleate megagametophyte may often divide aberrantly, giving rise to two partially degenerated nuclei, or it may degenerate without dividing, so that the mature gametophyte has only one "normal" antipodal cell. Because of the widely scattered distribution of certain of the different types, it would appear that they had arisen independently in several families.

In spite of differences in pattern of development, the basic organization of the mature megagametophyte is amazingly constant, and it is in most cases not possible to determine the type of developmental pattern by observation of the mature structure. *Polygonum*, *Allium*, *Fritillaria* and *Adoxa* types of development

all give rise to a similar gametophyte, and if one remembers that the antipodal cells are often ephemeral in any of these types and are commonly so in the *Drusa* type, and also remembers that the polar nuclei usually fuse, it then becomes impossible to be sure whether development follows one of the first four, the *Drusa*, or the *Oenothera* pattern without seeing the critical developmental stages.

The initiation of endosperm by a second fertilization—the fusion of the second male gamete with the polar nuclei—is a constant feature of normal sexual reproduction in angiosperms and serves to distinguish them from all other plant taxa. The chromosome number of the endosperm nuclei is not constant, however. Because of the origin of the endosperm from the polar nuclei of the megagametophyte plus one 1*n* male nucleus, its ploidy varies with the number and ploidy of the polar nuclei and is thus related directly to the type of megagametophyte development. Endosperm is most commonly 3*n* since two 1*n* polar nuclei are found in gametophytes of the *Polygonum*, *Allium*, *Drusa*, and *Adoxa* types. It will be 2*n* in *Oenothera* type gametophytes where there is a single 1*n* polar nucleus. It is 5*n* in gametophytes of the *Penaea* and *Plumbago* types where there are four 1*n* polar nuclei and also in the *Fritillaria* and *Plumbagella* types in which there are only two polar nuclei but one is 3*n* and the other 1*n*. The ploidy may be 8, 9 or 15*n* in different variations of the *Peperomia* type, the 15*n* occurring in *Peperomia hispidula* in which the megagametophyte has 1 synergid, 1 egg, 14 polar nuclei and 0 antipodal cells.

As was shown earlier, development of the endosperm may follow one of three patterns, and cellular endosperm is primarily a characteristic of the dicots and helobial of the monocots; in both classes other families have a nuclear type of development. Within the Liliatae and Magnoliatae cellular and helobial endosperm are not distributed evenly throughout the different subclasses. Among the monocots, helobial endosperm is most characteristic of the Alismidae (includes the old Helobiales from which the type takes its name), frequent in the Liliidae, and is not found in any family of the Arecidae. It is in the latter subclass that the only two monocot families with a cellular endosperm development—the Araceae and Lemnaceae—are placed. Among the dicots, a preponderance of families in the Magnoliidae and Asteridae have a cellular endosperm development. Within the Dilleniidae and Rosidae where the endosperm of a fair number of families is cellular, distribution is again concentrated in certain areas—in the Ericanae of the Dilleniidae and in the Rosanae (particularly the Saxifragales), Aralianae, and Celastranae (primarily among the Santalales) of the Rosidae. Several families of the Ranunculidae also have a cellular endosperm only: Schisandraceae, Lardizabalaceae, Circaeastraceae, Sarraceniaceae, and perhaps also the Illiciaceae (Davis lists only cellular, but the Delhi seminar synopsis lists both cellular and nuclear). Thus it can be seen that cellular endosperm might be said to have a bimodal distribution, occurring in several primitive families (Magnoliidae and Ranunculidae) and a larger number of derived families (Asteridae, Ericanae, Aralianae, Santalales) and only occasionally in more central families (Saxifragales). The cellular endosperm of the derived families frequently gives rise to haustoria, often both micropylar and chalazal; that of the primitive families only occasionally exhibits an haustorium; more commonly it does not. The "advanced" cellular endosperm,

with haustoria, commonly develops in the unitegmic, tenuinucellate ovules with an ephemeral nucellus and an endothelium which were discussed earlier.

Two divergent views have been expressed as to the direction of evolution of the endosperm. Some have held that nuclear development is primitive and others that cellular is the original type. In this connection Cronquist (1968) pointed out that it seems clear that in the Gentianaceae nuclear endosperm, characteristic of most of the family, is primitive and the cellular development found in *Voyria* and *Voyriella* is advanced. These genera lack chlorophyll and show other specialized features. He thought it unlikely that such specialized genera would have retained a primitive character (if cellular endosperm were primitive) that had been lost in the rest of the family. What is true for one family need not be true for the angiosperms as a whole, however. Sporne (1954) found nuclear endosperm development in dicotyledons to be statistically correlated with a variety of floral and vegetative characters: woody habit, secretory cells in leaves, stipules present, stamens pleiomerous, ovules with two integuments, and integuments with vascular bundles. He had earlier shown these characteristics to be part of a broader character-correlation which he interpreted as primitive. Accordingly, he concluded that nuclear endosperm should also be considered primitive. This conclusion was criticized by Swamy & Ganapathy (1957). Sporne (1967) conducted further statistical analyses including, among other new characters, features of the xylem. Four xylem characters were highly correlated and are generally accepted as primitive. Nuclear endosperm correlated negatively with two of these. Taken alone these negative correlations would suggest that nuclear endosperm was advanced. Sporne pointed out, however, that nuclear endosperm was positively correlated with ten characters (adding leaves alternate, petals free, and seeds arillate to the list above) which themselves were positively correlated (often with a very much higher positive correlation than the two negative ones) with primitive xylem. Nuclear endosperm was still suggested as primitive but the two negative correlations remained unexplained.

Lowe (1961) statistically analyzed a considerable number of floral characteristics of monocotyledons and found 17 of them to be positively correlated and primitive for that class. Among the 17 characters six were embryological: pollen development simultaneous, megagametophyte monosporic, parietal cell formed, anatropous ovule, binucleate pollen, and endosperm cellular or helobial—the latter in direct contrast to Sporne's suggestion that nuclear endosperm is primitive in the dicots. If one accepts that monocots were derived from early dicot-like ancestors, it is difficult to accept a different type of endosperm development as being primitive in the two lines. Probably the strongest proponent for the cellular type of development being the primitive one is Wunderlich (1959). She gave data for all families known and compared endosperm development with ovule type throughout the angiosperms. Her analysis showed that crassinucellate ovules usually showed nuclear development and tenuinucellate ovules cellular. Certain families contradicted this relationship, particularly the "Polycarpicae." She felt that the original angiosperms possessed a crassinucellate, bitegmic ovule and cellular endosperm. During evolution of the ovule and endosperm, if the nucellus remained large or increased in size, as is the case in primitive families, space

relations favored the appearance of nuclear endosperm; thus nuclear endosperm appeared early in the evolution of angiosperms. Where the nucellus decreased in size and became tenuinucellate, the condition characterizing advanced families, development of the endosperm was inhibited because of the decreased space and endosperm development remained cellular.

Other variations among embryological characteristics could be related to the major angiosperm taxa, but those already discussed will suffice to show the extent to which embryology correlates with a natural classification. A few characters show a moderately clear segregation among the classes or subclasses, but others are rather evenly distributed throughout.

EMBRYOLOGY AT THE FAMILY AND LOWER TAXA LEVEL

It should have become clear in the course of the preceding discussions that embryological characteristics are much more constant for the family than for taxa at the higher levels. For all characteristics some families are variable and in these the genus is commonly constant. It is at approximately the level of the family that embryological characters have most frequently been used to supplement others in arriving at taxonomic conclusions; sometimes families within an order have been considered, sometimes tribes of a family, sometimes individual genera. A few examples will be mentioned briefly. Details of these and of additional cases can be found in papers by Maheshwari (1950, 1956, 1961, 1963a), Cave (1953), Kapil (1962), Johri (1963, 1967), and Bhojwani & Bhatnagar (1974).

Occasionally a single characteristic is particularly distinctive, as in the case of the Podostemaceae. In this famly no endosperm develops and a "pseudo-embryo sac," formed by the disintegration of nucellar cells immediately below the megagametophyte, apparently takes over the functions of the endosperm. This is unmatched in any other family. Another family recognizable by one individual characteristic is the Onagraceae. This is the only family with an *Oenothera* type of megagametophyte development and that type of development has been found in every member of the family studied. The removal of *Trapa* from the Onagraceae, where it had tentatively been placed by various authors, is strongly supported by its possession of a *Polygonum* type of development. The Cyperaceae is another family with a distinctive characteristic: its pollen grain. After the formation of the four microspore nuclei, three of them are cut off to one side of the pollen grain and only the fourth divides to form the tube and generative cells and then the two sperms. This "pseudomonad" or "cryptotetrad" is found in all Cyperaceae and elsewhere only in some of the Epacridaceae in which, besides other differences, the mature pollen is two- not three-celled. In all three families, although a single characteristic has been stressed, it occurs in combination with others which serve to characterize the family.

In other cases no single feature is by itself distinctive but a particular combination of characteristics occurs together so regularly as to be considered diagnostic. There are instances of this sort where embryological data have been used to support or suggest the removal of a genus (or group of genera) from one family into a new one of its own. Examples are the Butomaceae and Limnocharitaceae, Menyanthaceae and Gentianaceae, Sphenocleaceae and Campanulaceae, etc.

Such constellations of characters have played a role in rearrangements of genera among the various liliaceous subfamilies and tribes, and have strongly supported the classification of the Lemnaceae in the Arales rather than in the Alismales.

The taxon which I know best is an excellent example of the use of embryology for taxonomic purposes. Samuelsson (1913) recognized early that the Ericales were characterized by a distinctive battery of embryological characteristics. To the list already published (Maheshwari, 1950; Palser, 1961) can be added embryo development of the Solanad type (Johansen's system) or belonging to the 9th or 11th group (2nd period, megarchetype III; Souèges's system) since Veillet-Bartoszewska (1963) has followed embryogeny in several species. No one characteristic by itself can be considered diagnostic, and many of them are those prevalent among the dicots or at least among the sympetalous ones. A few of the features are less widely distributed: permanent tetrads, absence of a differentiated endothecium in the anther, shape of the mature megagametophyte, and the linear arrangement of the first four cells of the endosperm. The entire group of characters taken together, however, does not occur elsewhere among the angiosperms. Samuelsson first recognized this embryological syndrome on the basis of his own observations, supplemented by earlier ones, dealing with roughly 30 species. Study of many more species since that time, while turning up a few exceptions, has served primarily to add considerable support to the consistency with which this constellation of characteristics occurs in the order.

The mutual relationship among the Ericaceae, Epacridaceae, Pyrolaceae, Clethraceae, and also Vacciniaceae and Monotropaceae if they are segregated from the others, has long been recognized. Several small families have, at one time or another, been included with the central ones in the Ericales: Empetraceae, Lennoaceae, Diapensiaceae, Cyrillaceae, Grubbiaceae, and most recently (Takhtajan, 1969) the Saurauiaceae and Actinidiaceae. Samuelsson (1913) was the first to point out that the Empetraceae had ericalean embryology, and a recent paper (Vijayaraghavan, 1969) on one species of the Cyrillaceae lends support to the inclusion of this family in the order. What details are known of the embryology of the Actinidiaceae-Saurauiaceae (Schnarf, 1924; Souèges, 1943; Crété, 1944; Vijayaraghavan, 1965) and Grubbiaceae (Fagerlind, 1947; Johri & Bhatnagar, 1960) are not inconsistent with their inclusion in the Ericales (Takhtajan, 1969), although Cronquist (1968) retained the Actinidiaceae-Saurauiaceae in the Theales and the Grubbiaceae in the Santalales. On the other hand, what little embryological data there are for the Lennoaceae (Copeland, 1935) do not fit well with the ericalean characters and the family is now normally classed in the Polemoniales. All these families could well stand observation of more embryological details and additional species. The Diapensiaceae are better known (Samuelsson, 1913; Palser, 1963; Veillet-Bartoszewska, 1963; Yamazaki, 1966; Reynolds, 1968). They agree with the Ericales in those characters that are widely distributed such as two-celled pollen; unitegmic, tenuinucellate, anatropous ovule; *Polygonum* type of megagametophyte development formed from the chalazal spore of the tetrad; and cellular endosperm. They differ in a few of the common and all of the more unusual aspects: pollen is not in tetrads; an endothecium is differentiated; there is no endothelium although the nucellus doe<

disintegrate; the megagametophyte is oval rather than showing an enlarged micropylar end; the first four cells of the endosperm are rarely linear; there are no endosperm haustoria; and embryogeny, while classed as Solanad by Johansen's system, is distinct (3rd group, 1st period, megarchetype IV; Souèges's system). In addition, there are other differences in anther development and structure, etc. Accordingly, the family has been removed from the Ericales and assigned to an order of its own which, at least for the present, is retained close to the Ericales (Cronquist, 1968; Takhtajan, 1969).

All characteristics discussed so far have been major developmental patterns, and the smaller differences, such as the size and shape of the ovule or of the developing or mature megagametophyte, characteristics of individual cells (for example, the synergids or antipodals), the arrangement of the early cells of the cellular endosperm and origin of the associated haustoria, etc. have been disregarded. These characteristics show a great deal of variation, however, and might well prove useful for helping to determine relationships within families or genera, particularly where the grosser characteristics are consistent throughout the taxon. In this regard, Cave (1953: 140) has stated that "variation in the gametophyte generation would seem to be as important in the study of phylogeny of genera as changes in the sporophyte generation. Because of the extremely reduced nature of the angiosperm gametophyte, small variations have great significance in tracing relationships." The significance of variation in, for example, the *Polygonum* type of megagametophyte development was pointed out by Herr (1967), who wrote: "small alterations in the developmental pattern constitute variations of high magnitude in the light of extremely low levels of structural complexity." He was of the opinion that more attention to detail would probably result in more comprehensive delimitation of generic, specific, and even individual distinctions in the megagametophyte of angiosperms. This generalization was followed (Smith & Herr, 1971) by a quantitative analysis, for one species, of development of the ovule from initiation to early embryogeny. This led to the conclusion that the size of the developing megagametophyte merits attention and "should be accorded special attention in studies designed to clarify phylogenetic relationships on the basis of megagametophyte structure."

Data for this detailed sort of analysis have not been accumulated, as they have been for the grosser characteristics and, moreover, are frequently not available. The only light that I can throw on this subject comes from some of my own comparative studies within the Ericaceae. Megagametophyte development has been followed for several species in each of two tribes, the Andromedeae (Palser, 1952) and the Phyllodoceae (Ganapathy & Palser, 1964). Comparisons were at a general, not quantitative, level. Mature ovules and megagametophytes are diagrammed at the same magnification in the two papers. Some differences could be detected among the several genera of the Phyllodoceae, while in the Andromedeae several rather striking differences in ovule size and shape, megagametophyte size and shape, and/or cellular characteristics were apparent. These were correlated with individual genera or groups of genera and tied in remarkably well with proposed taxonomic relations within the tribe. These tribes afford evidence that details can be useful in emphasizing the presence or absence of

homogeneity within a group of supposedly closely related genera or in suggesting possible relationships among individuals within a larger taxon.

Although in the studies of Andromedeae and Phyllodoceae two or more species of several of the genera were observed, the comparisons are primarily of interest at the generic level. The question then arises, can a similar type of analysis be useful among species of a single genus? At the present time I am engaged, with W. R. and M. N. Philipson of New Zealand, in a comparison of the ovule and megagametophyte throughout the very large genus *Rhododendron.* This genus seems an appropriate one for this type of study. Not only does it show a great deal of gross variation but, because of its horticultural interest, it has received extensive study from the taxonomic point of view. Thus, any ovule variations found can be related to a rather well established intrageneric classification of species. Only one paper has been published (Palser et al., 1971) so far; this treats development of a single species in detail. Records of observations of over 125 species, giving essentially complete coverage of all subcategories recognized in the genus, are gradually accumulating. Since some of these records are in this country and others in New Zealand and the information contained has not yet been synthesized, what the outcome will be is not known. Differences definitely do exist, but whether these will show any correlation with taxonomic subdivisions of the genus remains to be seen.

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NOTE ADDED IN PROOF

Since this paper went to press, a discussion of the distribution among angiosperms of four of the embryological characteristics presented in some detail in the section starting on p. 633—bitegmic versus unitegmic ovules, crassinucellate versus tenuinucellate ovules, cellular and helobial versus nuclear endosperm development, and binucleate versus trinucleate pollen—has been published (Dahlgren, 1975). The author concluded that the condition given last above for each of the four characteristics is most probably the secondary state. The reader is referred to this paper for details not incorporated in the present article and for very informative diagrams.

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THE BASES OF ANGIOSPERM PHYLOGENY: ULTRASTRUCTURE[1,2]

H.-Dietmar Behnke[3]

Abstract

A classification of sieve-element plastids by their major accumulation of ergastic products (protein or starch) into P-type and S-type, based on the ultrastructural research of some 500 species, provides systematists with a new micromorphological character to be used for a reconsideration of the outline of some of the higher taxa in the Takhtajan system of Magnoliophyta. Plastid types are listed for families and orders of Liliopsida and the first four subclasses of Magnoliopsida. Of these, Magnoliidae and Caryophyllidae are discussed in greater detail. It is demonstrated that sieve-element plastids can contribute relevant data to the rearrangement of at least some of the taxa in question. In addition some remarks are made on possible phylogenetic trends among the different plastid types.

Ultrastructure is a rather new field contributing to plant systematics. Despite the comparatively short time which has passed since its introduction, various techniques have already been used very successfully to contribute valuable micromorphological characters to distinctive taxonomic problems.

Cole & Behnke (1975) gave a short synopsis of new characters derived from comparative studies with the electron microscope, and a detailed evaluation of their application to plant systematics is being prepared (Behnke & Cole, in preparation). The data presented so far clearly demonstrate that, unlike the situation with lower plants, ultrastructural characters in higher plant systematics are largely confined to results achieved with the scanning electron microscope. With its potentiality to disclose new dimensions of plant surface the scanning electron microscope greatly extends our knowledge of morphological differences. In all of the recent attempts to come to a natural and phylogenetic system of higher plants, and of Magnoliophyta (Angiospermae) in particular, morphological information still ranks very high. Consequently, the scanning electron microscope seems more adequate to systematists and has more readily been accepted by them than other ultrastructural tools such as the transmission electron microscope and the freeze etching device. Thus the former failure of ultrastructural research to contribute reliable characters to magnoliophytan systematics may in part be due to its restriction to the cellular and subcellular level of the transmission electron microscope. There are two major reasons which explain why, for a long period, transmission electron microscopy did not even provide minor characters of taxonomic significance to the classification of Magnoliophyta: (1) within any given tissue, cell organelles are considered to be uniform; and (2), the distribution

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[1] Participation in the Symposium of the A. I. B. S. meeting, Amherst, Massachusetts, 1973, was made possible during the tenure of a visiting professorship at the Department of Botany, University of Texas at Austin, Texas 78712.

[2] The author wishes to express his gratitude to Mrs. L. Pop for technical help during part of the unpublished investigations reported and to Mrs. D. Laupp during preparation of figures and line drawings for this paper.

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Ann. Missouri Bot. Gard. 62: 647–663. 1975.

in Magnoliophyta of the relatively few different species that have been investigated with respect to a certain tissue is random.

It therefore was an exciting experience when we first became aware of the applicability of ultrastructural data of sieve-element plastids to taxonomic problems (Behnke, 1967, 1969a). Continued research on a gradually expanding number of species and higher taxa supported and substantiated our concept of the new micromorphological character in seed plant systematics. Application and reliability of sieve-element plastid ultrastructure to systematic and phylogenetic questions in Magnoliophyta is presented in this contribution to the symposium.

Since the present discussion will in general only descend to the family level, it may be convenient to refer to the detailed listing of species and references given in Behnke (1972) and to an additional list kept up-to-date by the author. The combined lists include ultrastructural data on more than 500 species.

TECHNIQUE

Sieve elements of any part of a plant can be used for a study of their plastids. Young stem parts are preferred in the majority of species investigated because of their easier handling, but roots, leaves, and flower stalks, which were used in some species, give equivalent results. In general, longitudinal hand sections of the appropriate plant part containing vascular bundles are fixed in a formaldehyde-glutaraldehyde mixture followed by treatment with osmic acid (for details see Behnke, 1975a). After dehydration in acetone, sections are recut into small phloem-containing pieces just before polymerization in epoxy resins. Trimming of the polymerized material proceeds with the control of a binocular microscope so as to obtain a top plane with less than 100 μm side length and with sieve elements in its center. Ultrathin sections (thickness about 50 nm), cut with glass or diamond knives, are viewed and photographed with a transmission electron microscope at varying magnifications (5–40,000 $\times$ in general). Determination of accumulation products within sieve-element plastids is done by specific staining reactions in light microscopic monitor sections, by enzymatic digestion within the ultrathin section (Behnke, 1967, 1975a), and occasionally by comparing their staining response to fixatives and contrast-enhancing material under the electron microscope with those of well-known examples.

PRINCIPAL CHARACTERS OF PHYLOGENETIC SIGNIFICANCE

Plastids are among the normal and continuous constituents of each living plant cell. Though there are different classes of plastids within different cells and tissues—e.g., chloroplasts, chromoplasts, or leucoplasts—a plastid can only be derived from a plastid of either the same or another class. Furthermore, it should be stressed at the very beginning that throughout the following discussion we will deal exclusively with *sieve-element* plastids. There are other plastids or other organelles that show structural differences on the inter- or intraspecies levels, but sieve-element plastids presently are the only organelle type that can be used as a structural character for considerations of the classification of higher taxonomic levels throughout Spermatophyta.

Sieve-element plastids are to be classified as leucoplasts, the class of non-

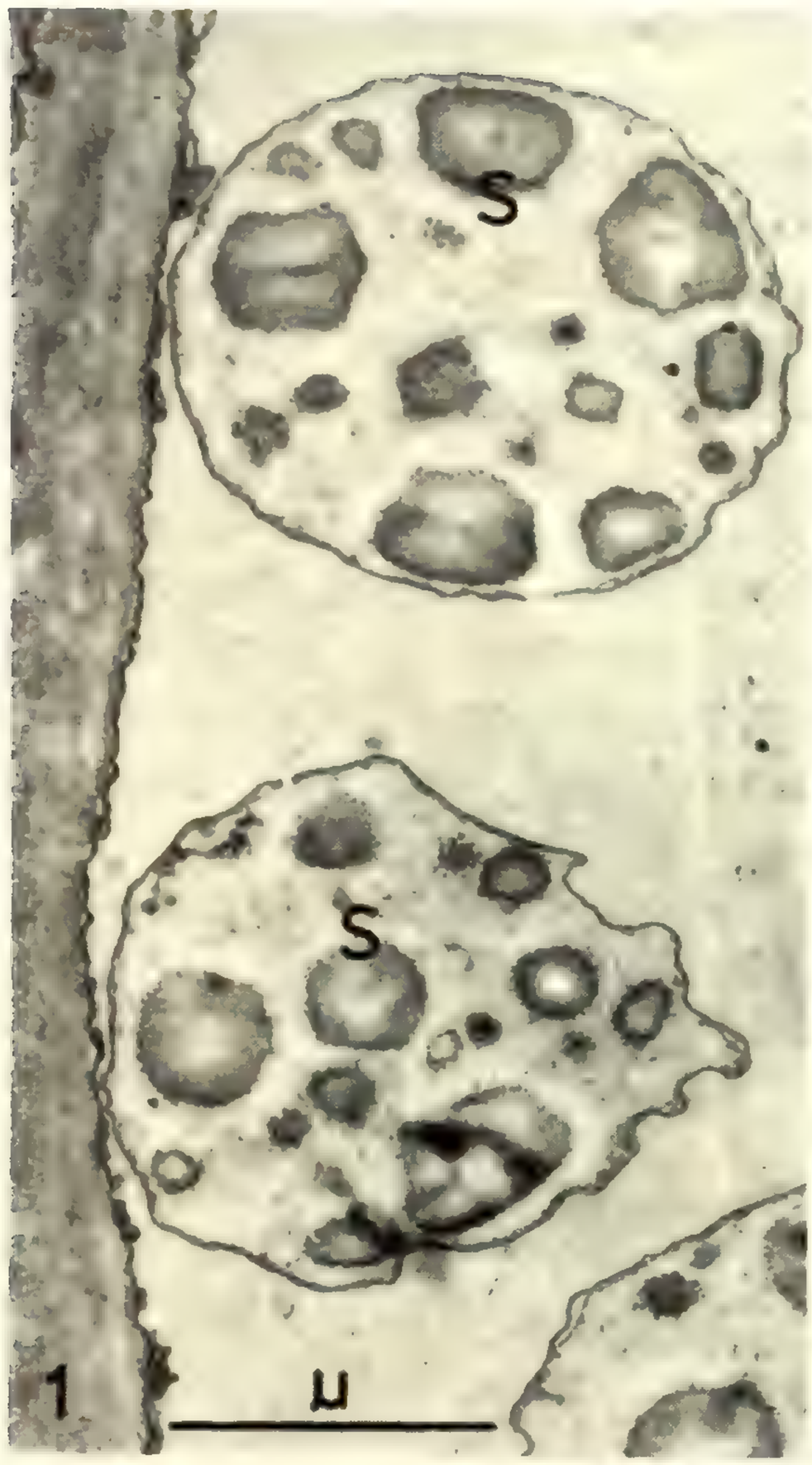
pigmented plastids. They are often called 'juvenile leucoplasts' because of their low degree of differentiation and deviation from proplastids, the plastids of meristematic cells. Plastids of phloem cells adjoining the sieve elements may have quite a different structure, e.g., there are chloroplasts in phloem-parenchyma cells. A common proplastid, elongated and amoeboid, with a dense inner matrix including some thylakoids, and surrounded by a double envelope, is the source of the different types of sieve-element plastids. During the differentiation of the sieve elements these proplastids show a gradual decline in matrix contents, an associated accumulation of ergastic storage material, and a transformation of their shape from oblong-amoeboid to spherical forms (Behnke, 1969a, 1969b). The differentiated plastids survive all structural and functional changes within the sieve element and do not disintegrate before final obliteration of the sieve element, e.g., at the end of a season. Therefore, taxonomic characters that are based on the structure of sieve-element plastids should be reasonably reliable. Such structural characters considered of taxonomic importance are the major products of ergastic accumulation, viz., sieve-element starch and protein. The amount of starch and protein, respectively, that is accumulated in the sieve-element plastids has been used as an aid for the artificial distinction of plastid types proposed by Behnke (1971a):

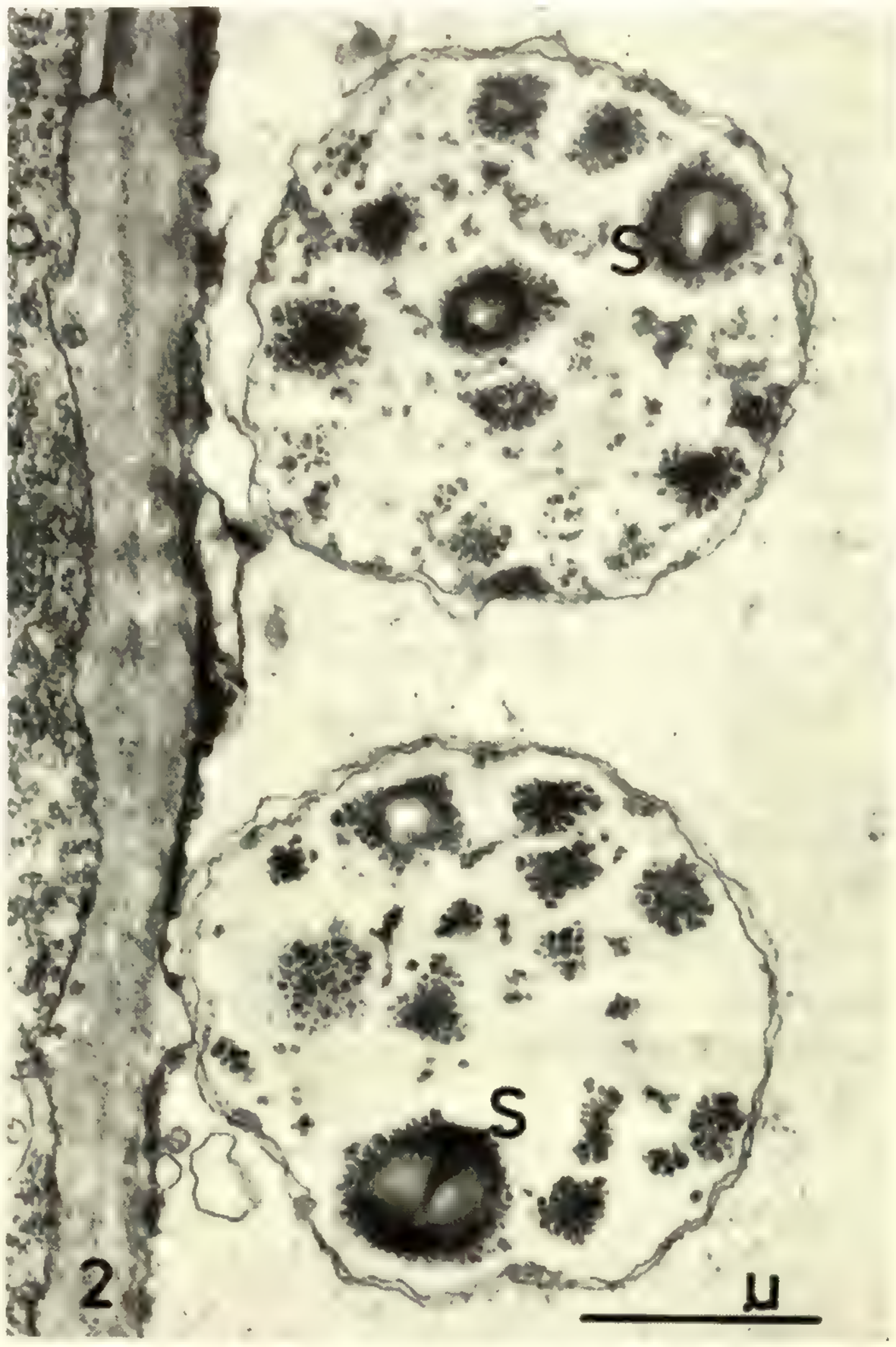
S-type plastids (Figs. 1–3) are defined as sieve-element plastids that accumulate starch as the main storage product (an accumulation of protein is not perceptible).

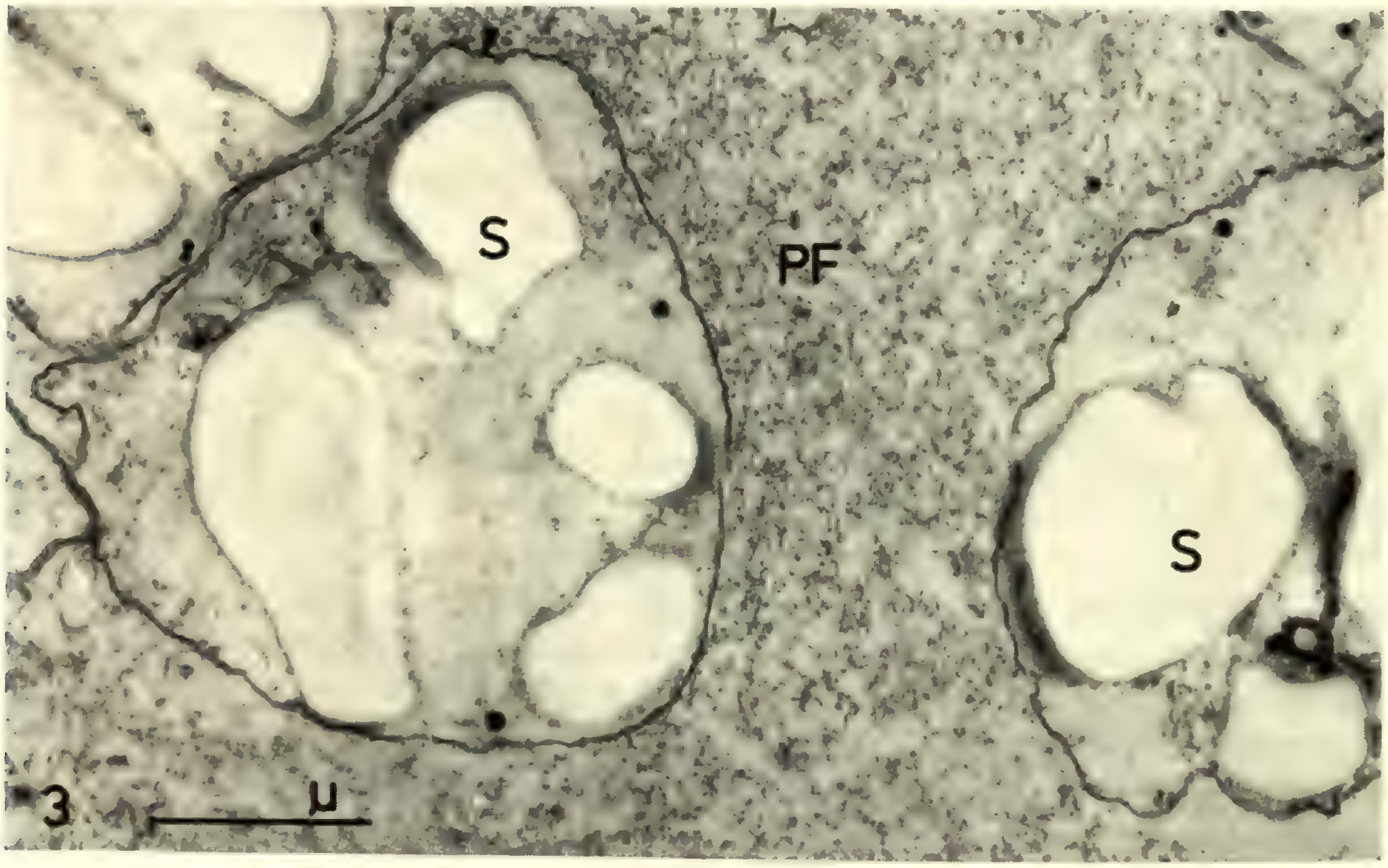
P-type plastids (Figs. 4–17) are defined as sieve-element plastids that accumulate protein as single product or in addition to starch. The ultrastructural morphology of the protein inclusions (their sizes, forms, and arrangement within the plastid) are used for a characterization of taxon-specific sub-types of protein accumulating plastids (Behnke, 1975a).

Starch in sieve-element plastids is deposited as single grains differing in number, size, shape, and stainability as seen with the electron microscope, and each species obviously has its own genetically defined type of starch grain (Badenhuizen, 1973), Figs. 1–3. There are some indications that the morphology of starch grains in sieve-element plastids may turn out to be specific for some taxonomic levels (Palevitz, unpublished data on Fabales; Behnke & Paliwal, 1973; Behnke, 1974a), but investigations at the present time are too scanty to firmly establish this. Moreover, the structural changes of starch grains during sieve-element aging may also play an important role. The chemical composition of sieve-element starch is apparently different from ordinary starch as demonstrated by sequential enzymatic digestion (Palevitz & Newcomb, 1970).

Protein accumulations in sieve-element plastids are present in the form of filaments or crystalline inclusion bodies, both being arranged in various ways, but the latter is in many cases presumably derived from the former (Figs. 4–17). Some forms of protein inclusions are typically restricted to some taxa of different taxonomic levels and can be defined as sub-types of the P-type plastids. These plastid inclusions have been identified as protein by enzymatic digestion with proteases (Behnke, 1975a), by their specific staining response against mercuric







FIGURES 1–3. Sieve-element plastids of the S-type with many starch grains (S).—1. *Ocotea foetens* (Lauraceae); × 22,000.—2. *Cocculus trilobus* (Menispermaceae); × 18,000.—3. *Cassytha filiformis* (Lauraceae); × 20,000. PF = protein filaments within sieve-element protoplasm.

bromphenol blue, and by their reaction in $KMnO_4$ fixatives (for references see Behnke, 1972).

Comparative Ultrastructure of Sieve-Element Plastids and the Takhtajan-Cronquist System of Classification of Magnoliophyta (Angiosperms)[4]

Class level: Magnoliopsida (dicotyledons) versus Liliopsida (monocotyledons)

Within Liliopsida sieve-element plastids have a highly uniform structure (Figs. 4–5), as far as can be determined from the diverse taxa investigated. Among Magnoliopsida, on the other hand, all of the different P- and S-type plastids currently known are recorded in the sieve elements of one taxon or another, some subtypes being closely restricted to individual taxa. Concerning the structure of the sieve-element plastids, only one investigation in the Magnoliopsida has come to our attention that shows an obvious homology to specific P-type plastids in Liliopsida: *Asarum* (four species investigated) of the Aristolochiaceae has the same cuneate protein crystalloids (subtype P:vcC)[5] with similar reactions to proteinase digestion and presumably the same pattern of arrangement as shown for Liliopsida (Fig. 13; Behnke, 1971b, 1975a). Unlike plastid types of Magnoliopsida, a relation between the P-type specific to Liliopsida and sieve-elements of Gymnospermae could not be found. Hence judging from the present available data on ultrastructure of sieve-element plastids, Liliopsida are a comparatively uniform and settled taxonomic group.

Subclass level

Magnoliopsida.—Our knowledge concerning the ultrastructure of sieve-element plastids of Magnoliopsida presently extends to more than 400 species belonging to some 110 families of 52 of the 73 orders. Nearly 200 species contain P-type plastids, but they come from only 31 families of 9 orders. However, it should be mentioned that intensive research has only been done with the first four subclasses (Magnoliidae through Caryophyllidae). Two of them (Ranunculidae and Hamamelididae) almost exclusively contain S-type plastids, Ranunculidae being the subclass of Magnoliopsida with the highest degree of homogeneity (100% S-type according to present information). Caryophyllidae and Magnoliidae show a large diversity in distribution of plastid-types and attain the maximum mixture of plastid-types in Magnoliidae. There is not much that can be said about supporting or opposing the composition of the subclasses as defined by Takhtajan (1973). The occurrence of only S-type plastids in Ranunculidae and Hamamelididae emphasizes the uniformity of these subclasses. But we can not easily make a distinction between them since ultrastructure so far does not provide criteria for a subdivision of S-type plastids.

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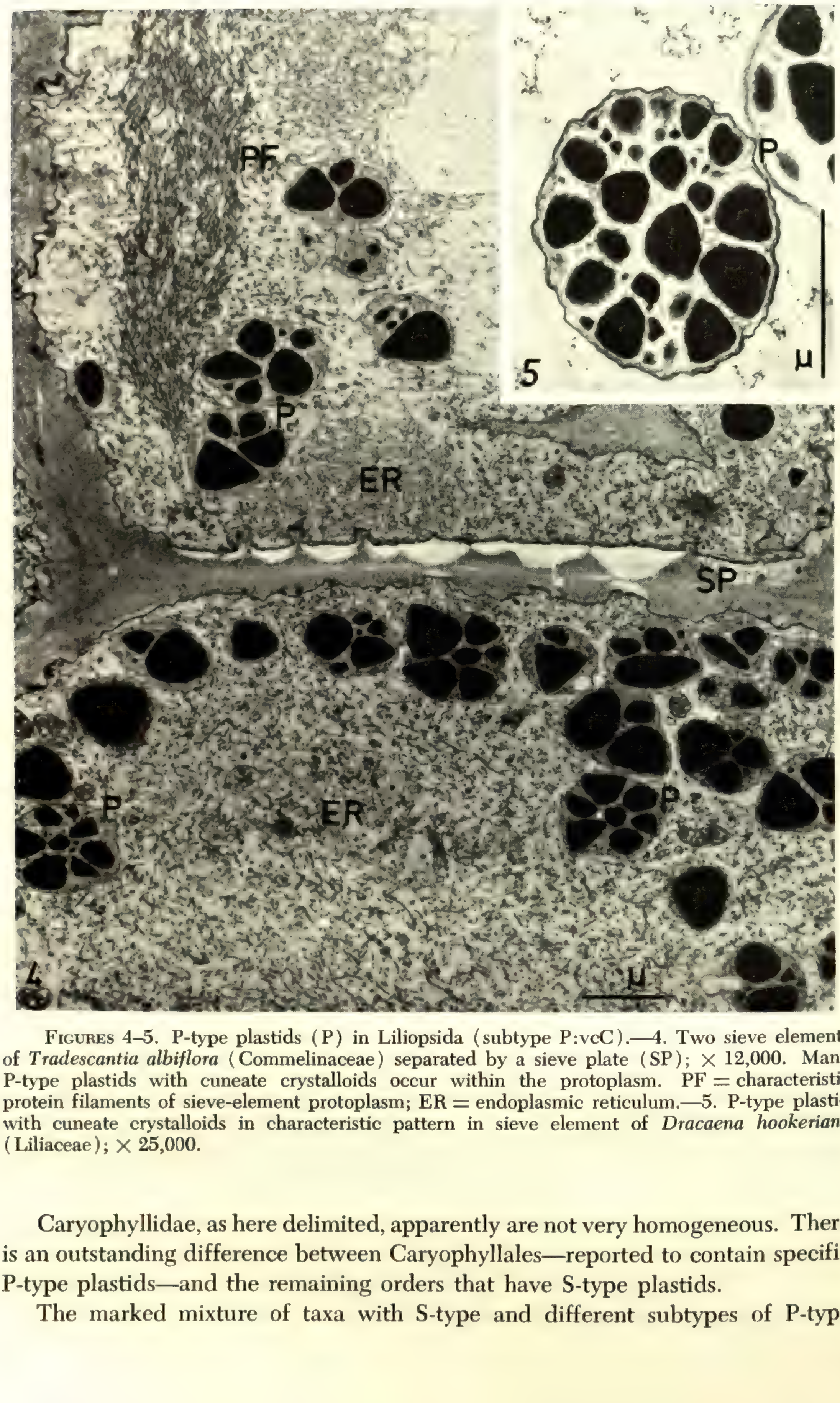
[4] The taxa used down to the family level, and their systematic arrangement follow the latest version of Takhtajan's (1973) system of flowering plants.

[5] Classification of subtypes after Behnke (1975a).



FIGURES 4–5. P-type plastids (P) in Liliopsida (subtype P:vcC).—4. Two sieve elements of *Tradescantia albiflora* (Commelinaceae) separated by a sieve plate (SP); × 12,000. Many P-type plastids with cuneate crystalloids occur within the protoplasm. PF = characteristic protein filaments of sieve-element protoplasm; ER = endoplasmic reticulum.—5. P-type plastid with cuneate crystalloids in characteristic pattern in sieve element of *Dracaena hookeriana* (Liliaceae); × 25,000.

Caryophyllidae, as here delimited, apparently are not very homogeneous. There is an outstanding difference between Caryophyllales—reported to contain specific P-type plastids—and the remaining orders that have S-type plastids.

The marked mixture of taxa with S-type and different subtypes of P-type

TABLE 1. P-type sieve-element plastids (subtype P:cvC [S]) in orders of Liliopsida.[a] (Figures following the orders represent the number of investigated families/genera/species.)

74. Alismales	3/3/3	84. Bromeliales	1/3/3
75. Hydrocharitales	1/1/1	85. Commelinales	1/4/4
76. Najadales	1/1/1	86. Eriocaulales	1/1/1
77. Triuridales	—	87. Restionales	3/3/3
78. Liliales	9/21/26	88. Poales	1/9/10
79. Iridales	1/1/1	89. Arecales	1/11/19
80. Zingiberales	4/4/5	90. Cyclanthales	1/1/1
81. Orchidales	1/5/5	91. Arales	2/4/4
82. Juncales	1/2/2	92. Pandanales	1/1/1
83. Cyperales	1/1/1	93. Typhales	2/2/2
		TOTALS	36/78/93

[a] For references see Behnke (1972).

plastids that has been shown to occur in Magnoliidae is probably due to the basal position that this subclass is thought to occupy in the evolution of the flowering plants.

Liliopsida.—Among the 93 investigated species from the four subclasses there is high conformity in the structure of their sieve-element plastids (Table 1). The specific pattern of P-type plastids (subtype P:vcC[S]) in Liliopsida includes cuneate protein crystalloids that are most prominently oriented toward the center of the plastid matrix (Figs. 4–5). Sizes and number of crystalloids vary, as well as sizes of the plastids. Accumulation of starch in addition to that of protein is recorded for some families, including all of those looked at in Zingiberales and Arales. Although there are particular patterns that are common only to Zingiberales (see Behnke, 1972), the deposition of starch in sieve-element plastids of Liliopsida does not appear to have an important relation to taxonomic considerations. For example, there are members of the *Dioscorea* genus that accumulate starch and others that do not.

Investigated species of the order Poales (10) display a character that is probably order-specific: in addition to the class-specific cuneate crystalloid, there is a second protein inclusion composed of tubular subunits.

ORDINAL-INTERFAMILIAL LEVEL

Magnoliidae.—Species of 19 of the 29 families from all orders were investigated (Table 2). The uniformity of sieve-element plastid types for families is rather high (8 with P-type, 10 with S-type, only one with both), but among the orders, there is more diversity. Magnoliales and Laurales are quite well balanced between P- and S-type containing families, while Piperales and Nymphaeales have S-type, and Aristolochiales only P-type plastids. Neither starch nor protein could be detected in sieve-element plastids of Rafflesiales. It may be important to stress that the P-type order Aristolochiales is often looked upon as specifically related to Annonaceae—as for example, based on phytochemical investigations (Hegnauer, 1960)—which is among those families of Magnoliales that contain P-type plastids exclusively. The specific modification of sieve-element plastids in

TABLE 2. Sieve-element plastids in Magnoliidae.[a] (Figures following the families represent the number of investigated genera/species; P = P-type, S = S-type plastids.)

Order 1: Magnoliales	
Magnoliaceae	S 2/4
Eupomatiaceae	P 1/1
Annonaceae	P 5/9
Canellaceae	P 1/1
Myristicaceae	P 1/1
Winteraceae	S 2/2
Order 2: Laurales	
Austrobaileyaceae	S 1/1
Monimiaceae	P 4/5
Hernandiaceae	P 2/2[b]
Chloranthaceae	S 1/1
Calycanthaceae	P 2/4
Lauraceae	P 1/2
	S 7/8
Order 3: Piperales	
Saururaceae	S 2/2
Piperaceae	S 2/5
Order 4: Aristolochiales	
Aristolochiaceae	P 2/13
Order 5: Rafflesiales	
Rafflesiaceae	2/2[c]
Order 6: Nymphaeales	
Cabombaceae	S 1/1
Nymphaeaceae	S 2/2
Barclayaceae	S 1/1
TOTALS	P 19/38; S 21/27; 212[c]

[a] All investigations by the author.
[b] Investigations include *Sparatthantelium* (formerly placed in Gyrocarpaceae).
[c] Insufficient material, neither starch nor protein detected in sieve-element plastids.

Aristolochia (Fig. 11) almost equals that of *Annona* (P:1pC.S; Fig. 6), while *Asarum* has exactly the same type as monocotyledons (P:vcC; compare Fig. 5 and Fig. 13). The detection of P-type plastids in sieve-elements of Eupomatiaceae, Annonaceae, Canellaceae (Fig. 7), and Myristicaceae, although all with different subtypes, parallels chromosomal data reported and used for evolutionary considerations by Ehrendorfer et al. (1968).

In Laurales Ehrendorfer et al. (1968) assign the phylogenetic basis to Monimiaceae to which are connected (1) Calycanthaceae and (2) a more advanced group: Lauraceae—Hernandiaceae(–Gyrocarpaceae). It is of interest to state that these families are also connected by the formation of P-type sieve-element plastids (for different modifications see Figs. 8–10), while other groups contain S-type plastids (see Table 2). In Lauraceae, however, only *Laurus* was found to have P-type plastids.

Cronquist (1968), while discussing the different characters in favor of an intermediate position of Eupomatiaceae, in his synoptical arrangement of families associates this family to his lauraceous cluster. The P:vpC.S modification of its plastids is very like that of Monimiaceae (Fig. 8) and would favor a placement within Laurales.

Ranunculidae.—There is a 100% representation of S-type plastids among the 13 families investigated from the total of 16 families recorded by Takhtajan

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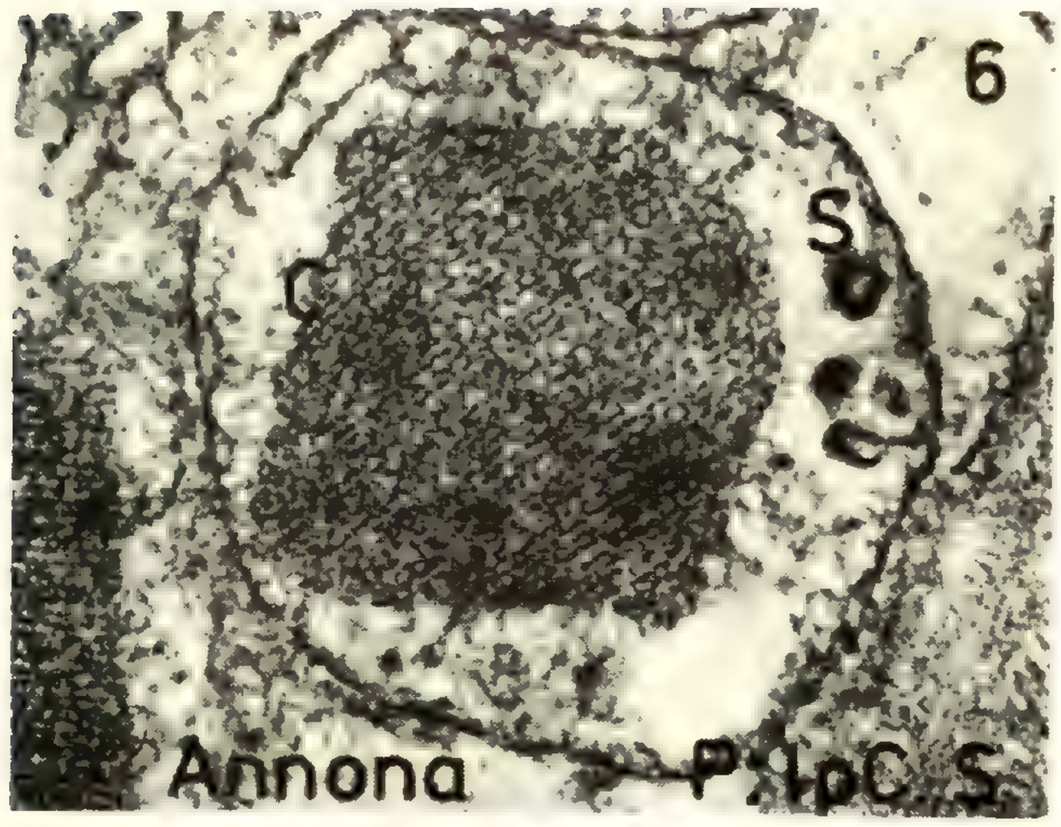
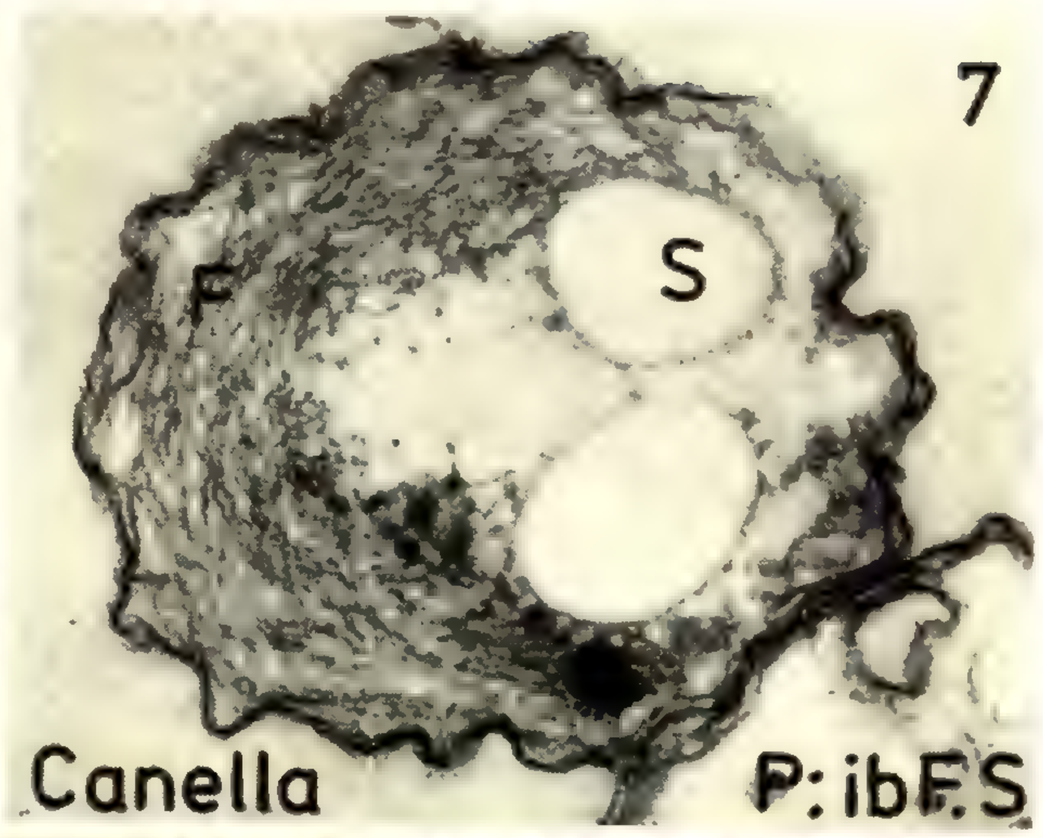
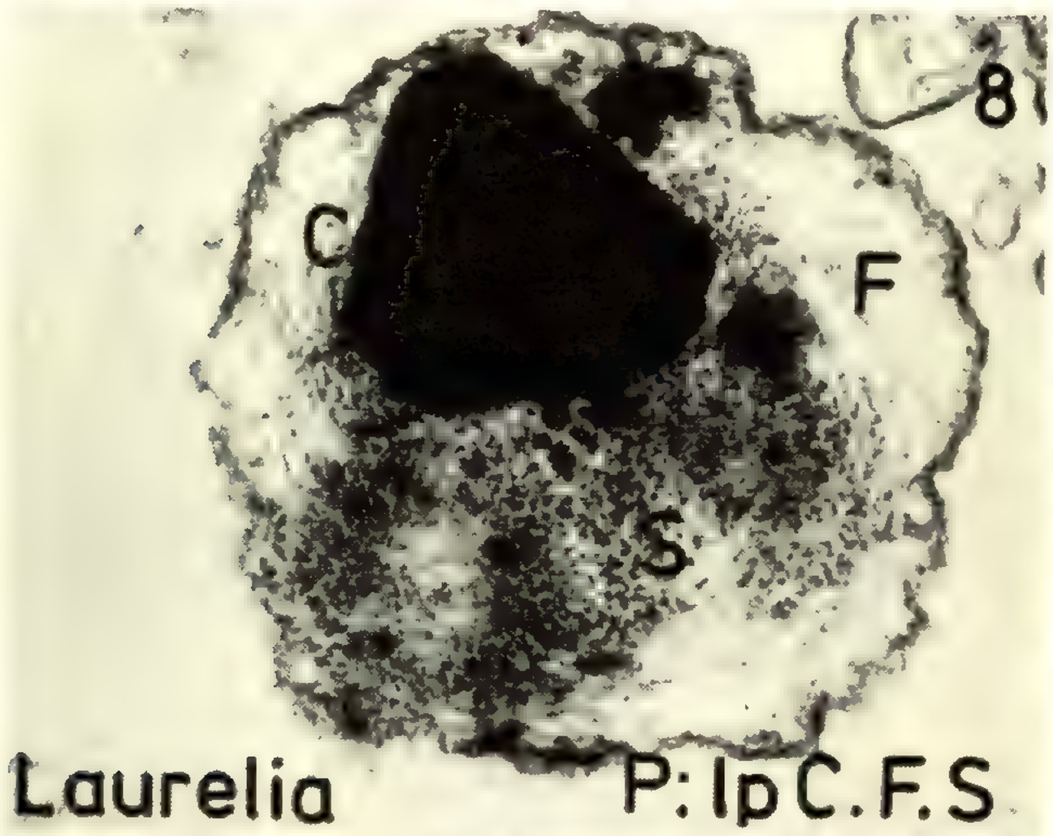
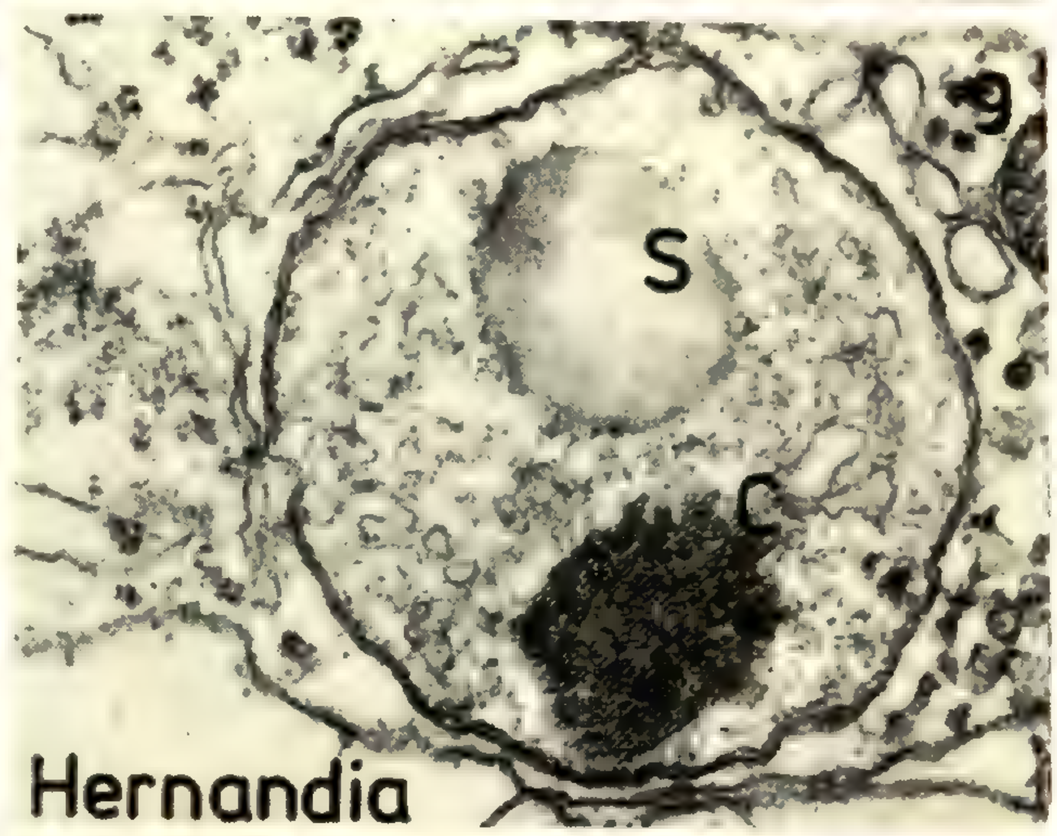
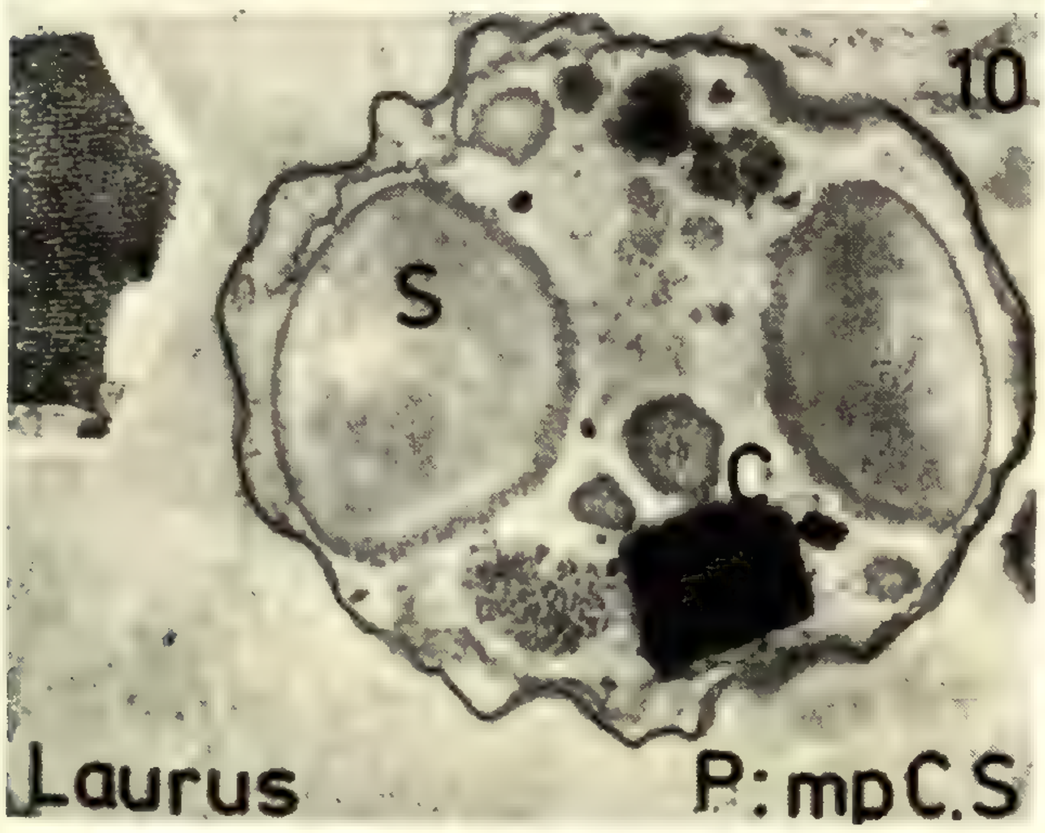
FIGURES 6–13. P-type sieve-element plastids of Magnoliidae. Diversity of subtypes is shown for three orders. For taxon-specific pattern, see individual figures.—6–7. Magnoliales.—8–10, 12. Laurales.—11, 13. Aristolochiales. b = bundle; C = crystalloid; c = cuneate; F = filaments; g = globular; i = irregular; l = large sized; m = minor sized; P = P-type; p = polygonal; v = variable.

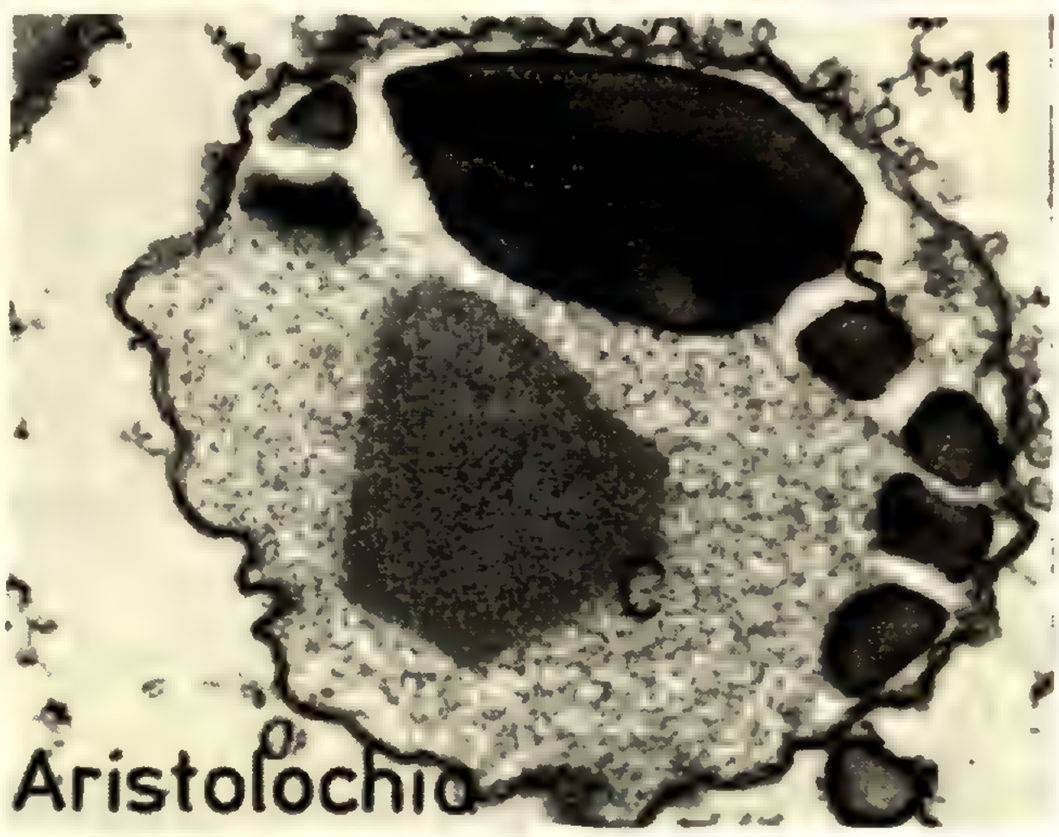

6
C
S
Annona P:lpC.S

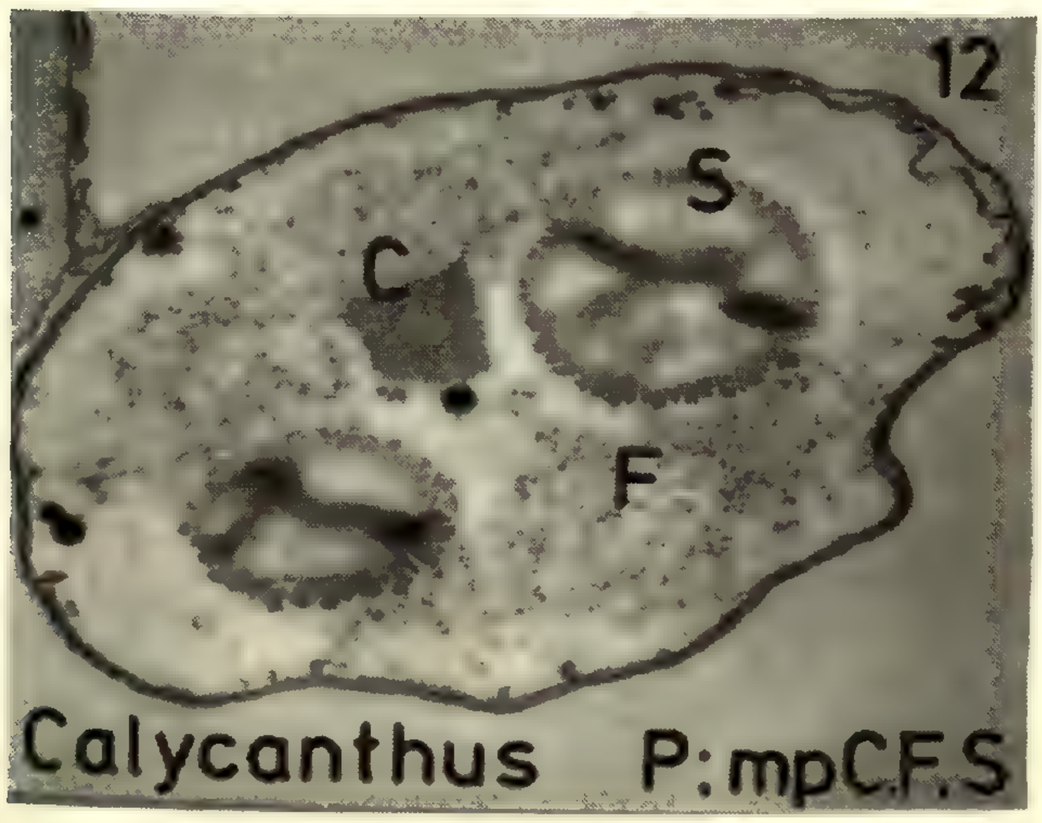

7
F
S
Canella P:ibF.S


8
C
F
S
Laurelia P:lpC.F.S


9
S
C
Hernandia


10
S
C
Laurus P:mpC.S


11
C
Aristolochia


12
S
C
F
Calycanthus P:mpCF.S

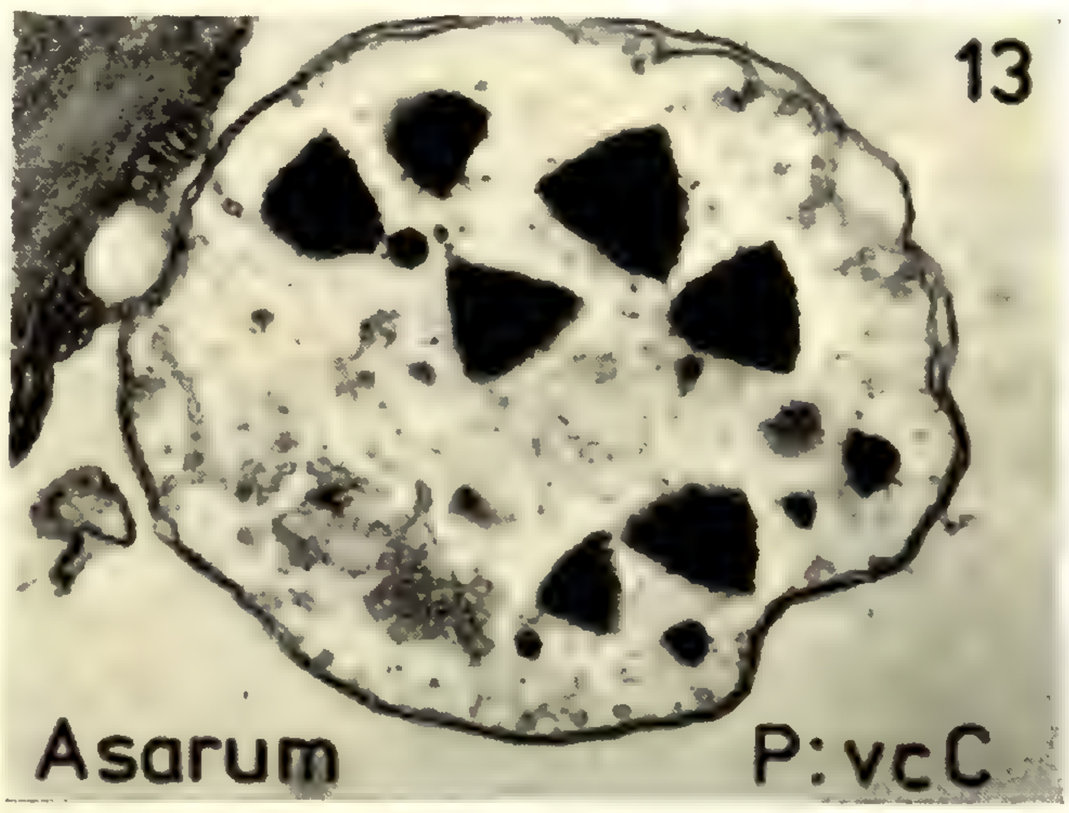

13
Asarum P:vcC

TABLE 3. S-type sieve-element plastids in Ranunculidae.[a] (Figures following the families represent the number of investigated genera/species.)

Order 7: Illiciales		Glaucidiaceae	1/1
Illiciaceae	1/1	Hydrastidaceae	1/1
Schisandraceae	2/2	Nandinaceae	1/1
		Berberidaceae	5/5
Order 8: Nelumbonales			
Nelumbonaceae	1/1	Order 10: Papaverales	
		Papaveraceae	1/1
Order 9: Ranunculales		Fumariaceae	1/1
Lardizabalaceae	3/3		
Menispermaceae	4/6	Order 11: Sarraceniales	
Ranunculaceae	4/5	Sarraceniaceae	1/1
		TOTALS 26/29	

[a] All investigations by the author, except for *Eranthis hiemalis* (Pacini & Cresti, 1972).

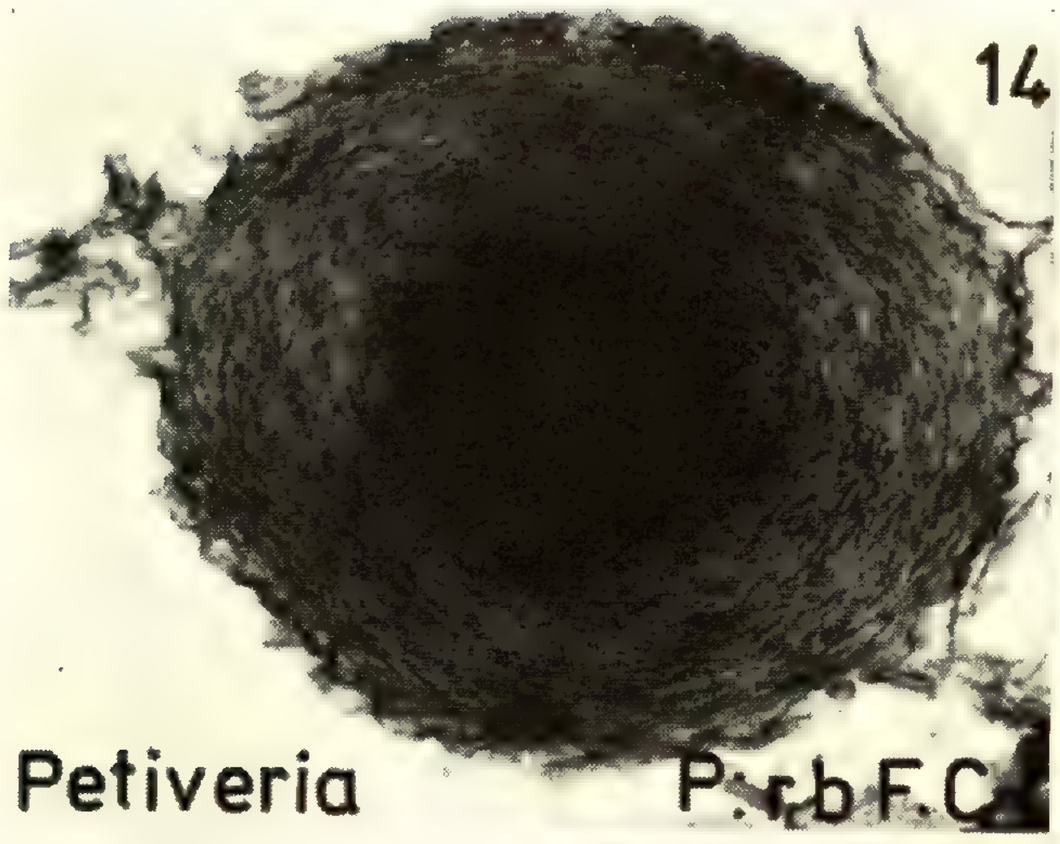
for this subclass (Table 3). However, as discussed previously, there is a limitation in the application of the ultrastructure of S-type sieve-element plastids to taxonomic problems below the subclass level in Ranunculidae.

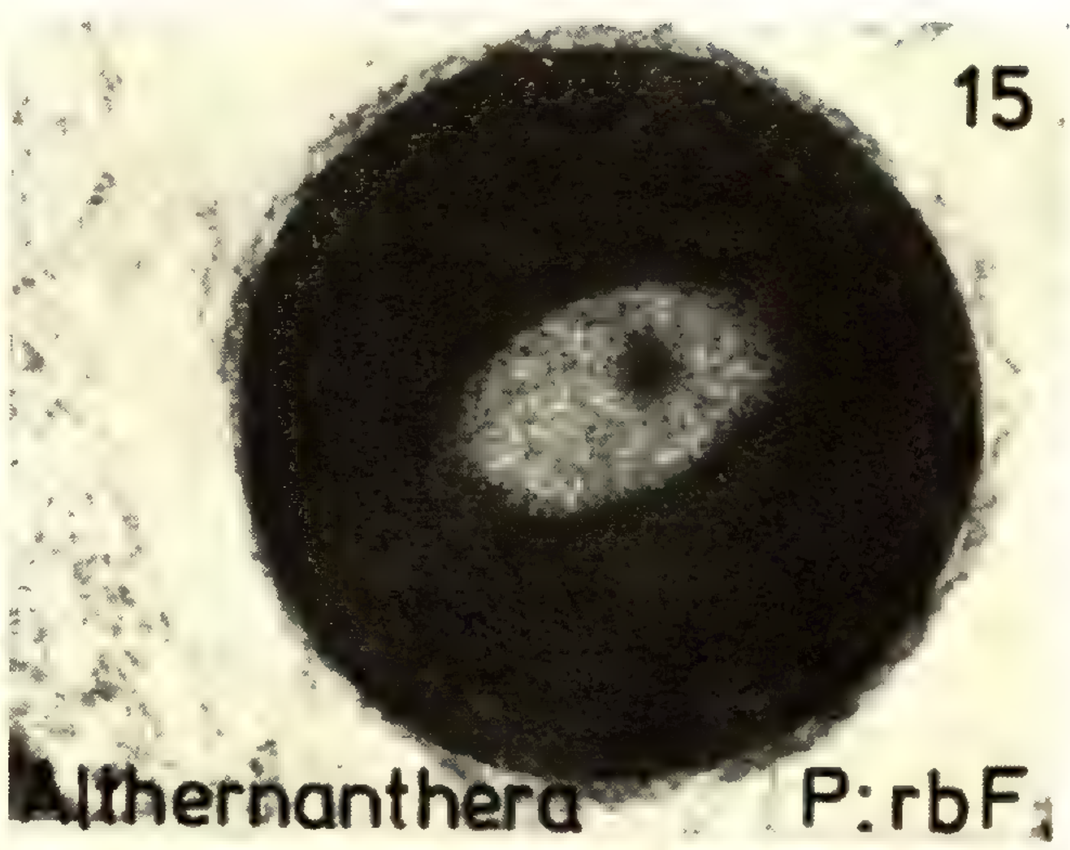
Hamamelididae.—This subclass, which according to ultrastructural data presented in Table 4 has a rather uniform distribution of S-type plastids, initially gave some problems in plastid classification during part of the studies performed (see Behnke, 1973). A number of species from Urticales, that had been reported in earlier light microscopic investigations to contain no plastids in their sieve-

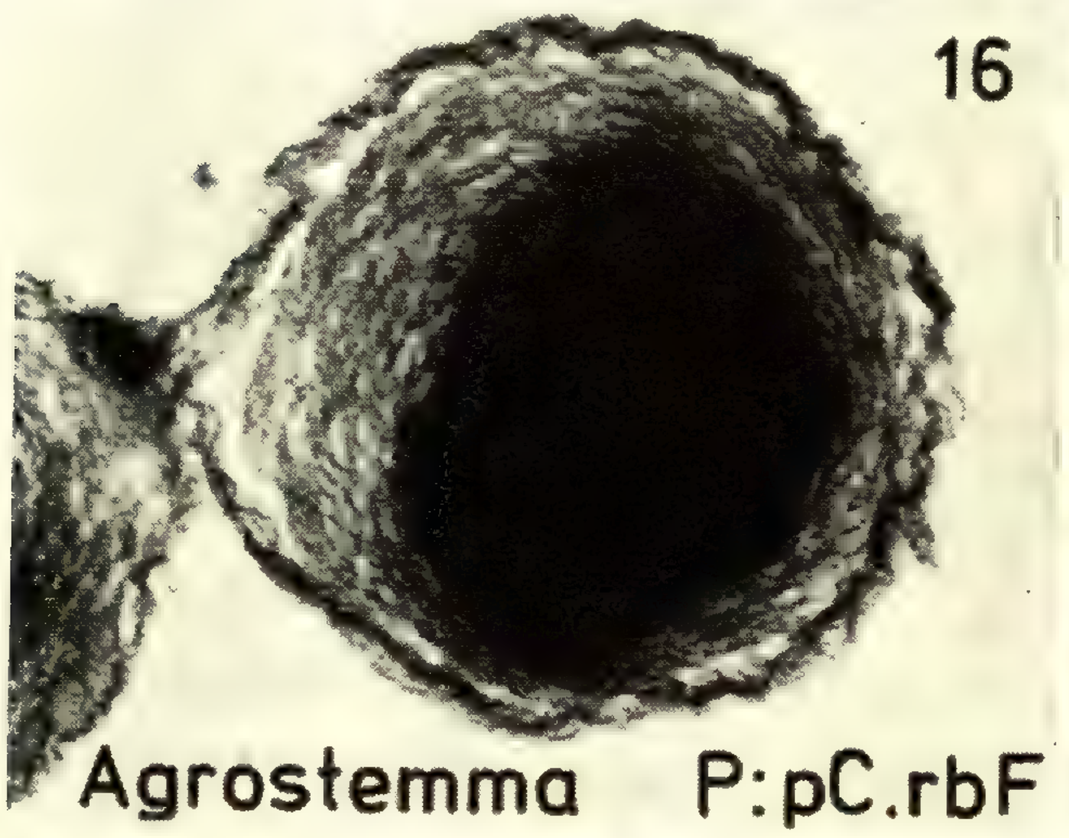
TABLE 4. Sieve-element plastids in Hamamelididae.[a] (Figures following the families represent the number of investigated genera/species; P = P-type, S = S-type plastids.)

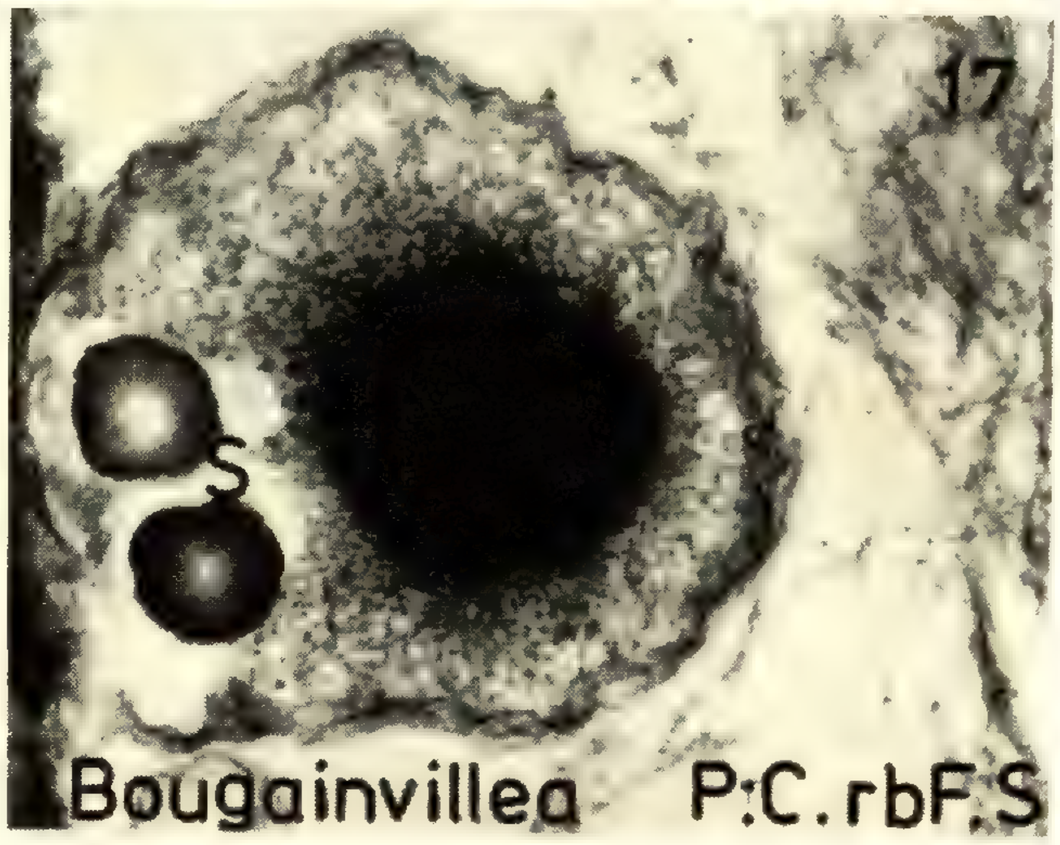
Order 12: Trochodendrales		Order 19: Barbeyales	
Trochodendraceae	S 1/1	Barbeyaceae	S 1/1
Order 13: Cercidiphyllales		Order 20: Casuarinales	
Cercidiphyllaceae	S 1/1	Casuarinaceae	S 1/2
Order 14: Eupteleales		Order 21: Fagales	
Eupteleaceae	S 1/1	Fagaceae	S 3/3
Order 16: Hamamelidales		Order 22: Betulales	
Hamamelidaceae	S 4/4	Betulaceae	S 5/5
Altingiaceae	S 1/1		
Platanaceae	S 1/1	Order 24: Myricales	
		Myricaceae	S 1/1
Order 17: Eucommiales			
Eucommiaceae	S 1/1	Order 25: Juglandales	
		Juglandaceae	S 3/3
Order 18: Urticales			
Ulmaceae	S 2/4	Order 26: Leitneriales	
(*Ulmus*)	P 1/3	Leitneriaceae	S 1/1
Moraceae	S 5/6		
Cannabaceae	S 2/2		
Urticaceae	S 8/9		
TOTALS S 42/47; P 1/3			

[a] All investigations by the author, except for *Ulmus americana* (Evert & Deshpande, 1969).









FIGURES 14–17. P-type sieve-element plastids of Caryophyllales; general subtype, P:g/pC.rbF.—14. Globular crystalloid.—15. Variation P:rbF; no crystalloids in Amaranthaceae and Chenopodiaceae.—16. Variation P:pC.rbF; central crystalloids polygonal in Caryophyllaceae.—17. Variation P:C.rbF.S; starch in addition to crystalloids and filaments (of minor taxonomic importance).

elements, displayed plastids during ultrastructural studies but turned out to lack any prominent storage product. Since a thorough investigation then revealed at least some starch in some of these species, they were classified as having S-type plastids (Behnke, 1973).

Only the genus *Ulmus* (3 species investigated) deviates from the general pattern of this subclass. First shown for *U. americana* by Evert & Deshpande (1969) and later affirmed for two more species by the author, this genus contains P-type plastids that elaborate distinct rhomboidal crystalloids. This feature is explained as the result of the independent origin of this character and is not related to its occurrence in other taxa.

Caryophyllidae.—Caryophyllidae are among those subclasses whose scope has been changed several times due to intense investigations of almost every character contributing to a taxonomic classification. Once a specific P-type plastid in the sieve-elements of a couple of species was observed (Behnke, 1969b), efforts were made in ultrastructural studies to cover the entire group including all of its different families (Behnke & Turner, 1971; Behnke, 1972, 1974b, unpublished data). Investigated were 130 species of 16 of the 17 families listed by Takhtajan

TABLE 5. Sieve-element plastids in Caryophyllidae.[a] (Figures following families represent the number of investigated genera/species.)

Sieve-element plastid types			
P-type		S-type	
Order 27: Caryophyllales		Order 27: Caryophyllales	
Phytolaccaceae	11/15	Gyrostemonaceae	1/1
Nyctaginaceae	3/6	Bataceae	1/1
Molluginaceae	2/3		
Aizoaceae	11/12	Order 28: Polygonales	
Tetragoniaceae	1/2	Polygonaceae	2/3
Cactaceae	8/10		
Portulacaceae	10/19	Order 29: Plumbaginales	
Basellaceae	2/2	Plumbaginaceae	3/4
Didiereaceae	4/6		
Halophytaceae	1/1		
Hectorellaceae	1/1		
Caryophyllaceae	16/20		
Amaranthaceae	11/16		
Chenopodiaceae	12/15		
TOTALS P	93/128	TOTALS S	7/9

[a] All investigations by the author except for *Tetragonia expansa* (Falk, 1964), *Beta vulgaris* (Esau, 1965), *Polygonum fagopyrum* (Arsanto, 1970), *Echinomastus intertextus* (Riviera, personal communication), *Opuntia subulata* (Delay & Darmanaden, 1973).

(1973) under the order Caryophyllales (see Table 5), and all of the families placed by Cronquist (1968) within the same order. Except for two families, all contained specific P-type plastids (P:rbF. [C.S]) characterized by peripheral ring-shaped bundles of protein filaments (Figs. 14–17) and often encircling an additional crystalloid. This list includes all of those families that were shown to contain betalains (Mabry et al., 1972; Mabry, this symposium); genera that are sometimes segregated as families: Achatocarpaceae, Agdestidaceae, Petiveriaceae, Stegnospermaceae, Dysphaniaceae; and two anthocyanin-containing families: Caryophyllaceae (including Illecebraceae) and Molluginaceae.

There are some structural modifications within the Caryophyllales subtype of P-type plastids which distinguish some families: Chenopodiaceae and Amaranthaceae lack the central crystalloid (Behnke, 1974b). Their plastid subtype is P:rbF (Fig. 15). Caryophyllaceae can be distinguished from the other families by their polygonal crystalloid (Fig. 16: subtype P:pC.rbF). A more detailed description of family characteristics among Caryophyllales and their interrelationships is being prepared (Behnke, 1976a).

The plastid investigations once more gave strong evidence for the inclusion of the Cactaceae and Didiereaceae in the Caryophyllales, as was earlier indicated by morphological and phytochemical work (Rauh & Reznik, 1961; Mabry et al., 1963). From the same kind of investigations, however, evidence should be drawn to exclude Bataceae and Gyrostemonaceae from the Caryophyllales. These are the only families of Caryophyllales, sensu Takhtajan, that have S-type plastids (Behnke & Turner, 1971; Behnke, unpublished observations). Bataceae contain neither betalains nor anthocyanins (Mabry & Turner, 1964); in Gyrostemonaceae pigmented parts have not been found yet. Pollen morphology in Gyrostemonaceae

and Bataceae is unique and strictly different from Phytolaccaceae or other Caryophyllales (cf. Eckardt, 1964; Nowicke, 1975). This may be regarded as another point in favor of a separation of these families from the order Caryophyllales.

Cronquist (1968) raises Bataceae to the rank of a separate order Batales which he arranges with the S-type containing orders Polygonales and Plumbaginales following the order Caryophyllales. From the ultrastructural data on sieve-element plastids this alliance could be favored against Takhtajan's treatment, since it associates nearly all S-type containing taxa of the subclass Caryophyllidae.

Whether Bataceae should be moved to the Capparales as suggested by Schraudolf et al. (1972) based on the presence of myrosin, or kept among Caryophyllidae, should be decided by further investigations. Viewed from evidence of sieve-element plastid investigations, their alliance to Capparales would not be excluded. Species of this order have also been recorded to contain S-type plastids (Behnke, 1972).

Many genera that by some systematists were allied with Caryophyllidae (or Centrospermae) were also found to contain S-type sieve-element plastids:

(1) *Theligonum* was formerly treated as separate order following Plumbaginales. Recently authocyanins have been detected in this genus (Mabry et al., 1975). Strong evidence is accumulating from other phytochemical (Kooiman, 1971), as well as morphological and embryological (Wunderlich, 1971), investigations which indicates that Theligonaceae should be closely related to Rubiaceae. Sieve-element plastid investigations in this family demonstrated S-type plastids throughout (Behnke, 1975b).

(2) *Fouquieria* and (3) *Frankenia*, both belonging to Tamaricales and previously doubtfully allied to Centrospermae, contain S-type plastids (Behnke, 1976b).

(4) *Rhabdodendron*, associated to Centrospermae by Prance (1968), develops P-type plastids of a subtype not comparable to the Caryophyllales-type (Behnke, 1976b).

(5) *Viviania*, claimed by Bortenschlager (1967) to have pollen grains whose pollen morphology is like that of Phytolaccaceae, and listed as a separate family among Caryophyllales by Takhtajan (1973), was not available for ultrastructural studies of sieve-element plastids.

Concluding Remarks on Phylogeny of Magnoliophyta as Derived from Ultrastructure of Sieve-Element Plastids

Apart from the statement that there are some taxa with a fairly well restricted and specific plastid type, there are different possibilities of interpretation of how the present distribution of types of sieve-element plastids (Fig. 18) can be related to the phylogeny of Magnoliophyta. One interpretation is that all of the different patterns (S- as well as P-types) have an independent origin, an assumption that has been proven valuable for some other characters. We presently are inclined to follow another interpretation which presupposes a common origin of all of the plastid types. But as yet, we do not know what kind of common origin, that is, neither which plastid type arose first nor in which taxonomic group it arose. Our hypothesis is that accumulation of only one product—either starch or protein—is

THE DISTRIBUTION OF P-TYPE AND S-TYPE SIEVE-ELEMENT PLASTIDS IN SPERMATOPHYTA

Subclasses of MAGNOLIOPHYTINA arranged after TAKHTAJAN (1973), the size of the circles is proportional to the number of species, recounted from ENGLER's Syllabus

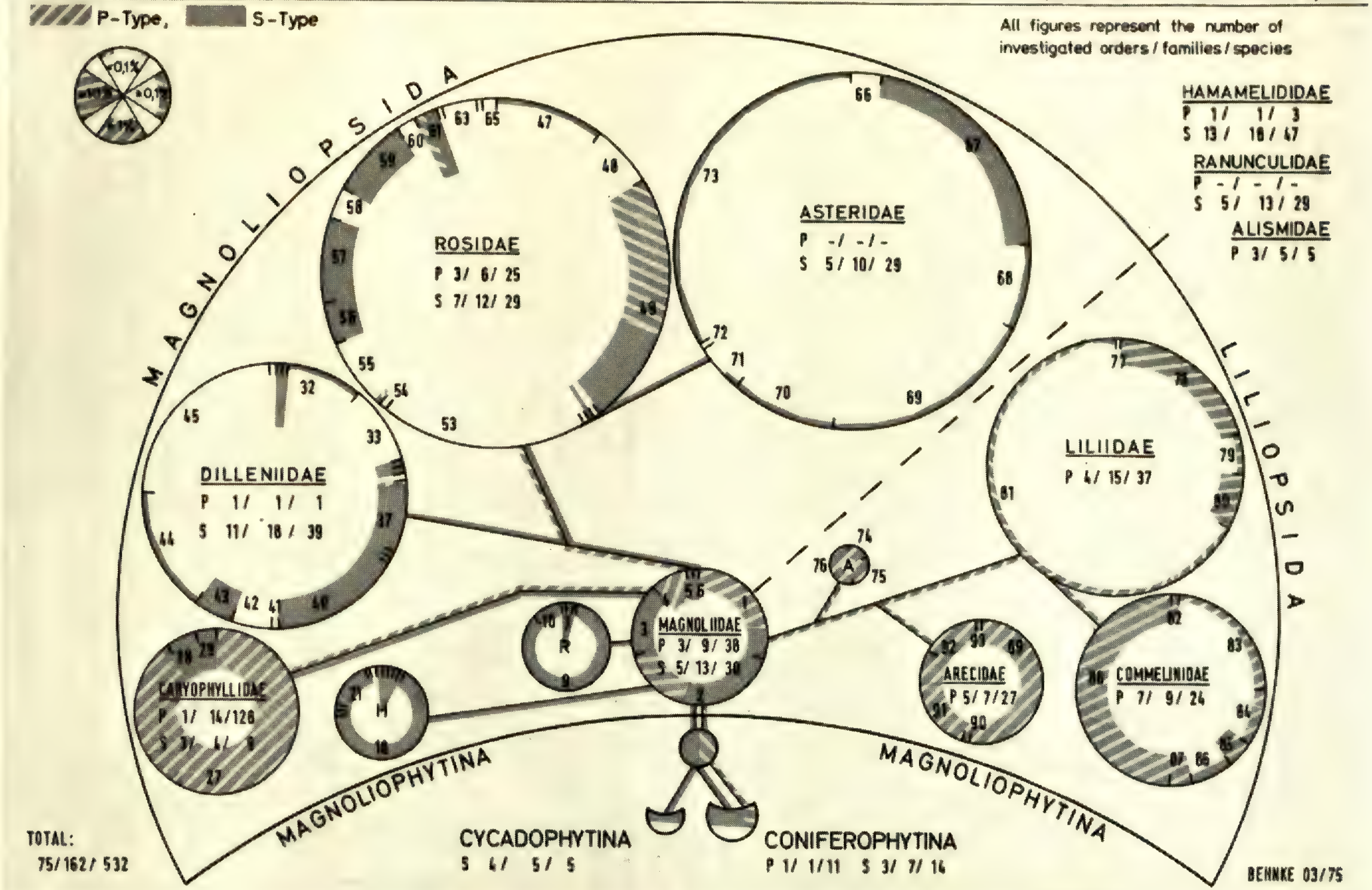


TABLE 6. Sieve-element plastids of Gymnospermae.[a] (Systematic arrangement after Ehrendorfer, 1971; figures following the families represent the number of investigated genera/species; P = P-type, S = S-type plastids.)

Coniferophytina	
1. Ginkgoatae	
Ginkoaceae	S 1/1
2. Pinatae	
Araucariaceae	S 1/1
Pinaceae	P 7/11
Taxodiaceae	S 4/4
Cupressaceae	S 4/4
Podocarpaceae	S 2/2
Cephalotaxaceae	S 1/1
3. Taxidae	
Taxaceae	S 1/1
Cycadophytina	
2. Cycadatae	
Cycadaceae	S 1/1
Zamiaceae	S 1/1
4. Gnetatae	
Ephedraceae	S 1/1
Welwitschiaceae	S 1/1
Gnetaceae	S 1/1
TOTALS	P 7/11; S 19/19

[a] For references see Behnke (1974a).

first, that the capacity to accumulate the other product is gained later, and that the synthetic activity for the original product is sometimes lost. Starch is the most common accumulation product in sieve-elements of lower vascular plants (Evert, personal communication) and Gymnospermae (Table 6) and this favors the S-type plastid as being the primitive one. In contrast to this, the reappearance of starch among P-type plants of some of the advanced orders of Liliopsida may provide evidence for the pure P-type plastid as being the primitive one. So far this can not be decided. The common origin, if any, should probably be sought in the groups traditionally thought to be closely related to angiosperm ancestors. But, if we adhere to a common line within the recent Magnoliophyta—independent of what was first, starch or protein—Caryophyllales can not easily be derived from the Ranunculales as proposed by Takhtajan (1973). Unless we suppose a second independent origin of Caryophyllales P-type plastids, they should be traced back directly to Magnoliidae or their ancestors. The latter is more likely since in Pinaceae (Table 6) there are P-type plastids (P:g/pC.rbF.S) that are very similar to the type of plastids in Caryophyllales.

The schematic representation of the distribution of types of sieve-element plastids among the subclasses of Magnoliophyta (investigated species expressed in percentage of recorded species) and the probable interrelationships between the plastid types as expressed in Fig. 18 follows only one line of interpretation and investigation. There are important arguments for the independent origin of the plastid types within different taxa. Further investigation in this field is hopefully expected to provide stronger evidence for one hypothesis or the other.

←

FIGURE 18. P- and S-type sieve elements in seed plants. Distribution of investigated species is given as a percentage of the total number of species by the shaded areas within the subclass circles (see percentage explanation in upper left circle). Peripheral figures within circles represent the numbering of orders after Takhtajan (1973).

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THE BASES OF ANGIOSPERM PHYLOGENY: PALYNOLOGY[1,2]

JAMES W. WALKER[3] AND JAMES A. DOYLE[4]

ABSTRACT

The field of palynology is reviewed in terms of its contributions to angiosperm systematics and phylogeny. Principal pollen characters which are phylogenetically useful at higher taxonomic levels (including aperture type, pollen wall architecture, pollen-unit, polarity, symmetry, shape, and grain size), and their evolutionary trends are examined. Many palynological characters and concepts are subjected to re-examination, particularly in an evolutionary-phylogenetic context. An attempt is made to show how pollen characters correlate with various higher categories of the Takhtajan and Cronquist systems of angiosperm classification and to outline certain phylogenetic trends observed in the pollen of different groups of angiosperms. With some exceptions, pollen morphology is consistent with the levels of relative advancement and the relationships postulated in the Takhtajan and Cronquist systems. Angiosperm pollen grains are clearly divisible into two fundamentally different types (each with its own derivatives): heteropolar, bilateral, boat-shaped *monosulcate* pollen versus isopolar, radiosymmetric, globose *tricolpate* pollen. "Gymnospermous" monosulcate pollen and derivative types (ulcerate, disulculate, etc.) characterize both the putatively primitive dicotyledonous subclass Magnoliidae and the monocotyledons. The six non-magnoliid dicotyledonous subclasses, on the other hand, are characterized by tricolpate pollen and derivative types (tricolporate, triporate, rugate, etc.). Relatively primitive tricolpate pollen is retained by many Ranunculidae,

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J. A. Doyle completed his part of this paper while an associate of the Laboratoire de Palynologie, C. N. R. S., Montpellier, France (M. Van Campo, Directeur), and wishes to thank Mme. Van Campo for her critical comments on the systematic section of the paper and for making available the facilities of the laboratory.

[2] The general introduction, principal phylogenetically useful pollen characters, comparative palynology of the subclass Magnoliidae, palynological technique, and major palynological reference works sections were prepared by J. W. Walker. The section on comparative palynology and the Takhtajan and Cronquist systems of angiosperm classification (exclusive of the subclass Magnoliidae) and the general summary and conclusions were prepared by J. A. Doyle.

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Caryophyllidae, and "lower" Hamamelididae. The Dilleniidae (except Dilleniaceae) and Rosidae are somewhat more advanced in having basically compound-aperturate tricolporate pollen. The subclass Asteridae, which retains indications of a rosid ancestry, exhibits the greatest array of specialized pollen types. The most important palynological contradiction of the Takhtajan and Cronquist systems is the fact that the highly specialized, basically triporate pollen of the "higher" Hamamelididae (Amentiferae) can be more directly related to triangular tricolporate pollen of the Rosidae than to the tricolpate pollen of the "lower" Hamamelididae. Briefer sections of the paper deal with pollen technique and the major reference works of systematic palynology.

Palynology (from the Greek words, to strew or sprinkle, fine meal; cognate with the Latin *pollen*, flour or dust) is the study of pollen and spores. Although paleontologists have extended its coverage to include organisms or parts of organisms that fall in the spore-pollen size range, such as coccolithophorids, dinoflagellates, diatoms, desmids, hystrichosphaerids, fungal elements, microforaminifera, radiolaria, etc., this paper is restricted to consideration of pollen of flowering plants, even though what is said may be related sometimes to the pollen of gymnosperms or even to pteridophyte spores. Among the bases of angiosperm phylogeny, palynology is unique in that through no other study can one obtain as great an amount of information from so little material in such short a time. Indeed, few fields of botanical inquiry permit as many specimens to be prepared and their variation observed as rapidly as the study of pollen morphology (cf. Van Campo, 1966).

The purpose of this paper is two-fold. First, principal pollen characters which are phylogenetically useful and their major evolutionary trends are examined. In this section many palynological characters and concepts are subjected to re-examination, particularly in the context of phylogeny and evolution. Secondly, an attempt is made to show how these pollen characters correlate with various higher categories in the Takhtajan (1969) and Cronquist (1968) systems of angiosperm classification and to outline certain phylogenetic trends observed in the pollen of different groups of angiosperms. Briefer sections treat palynological technique in general and major palynological reference works.

Principal Phylogenetically Useful Pollen Characters

Principal phylogenetically useful pollen characters and their evolutionary trends are discussed in this section. Pollen characters which are only of limited taxonomic importance at the generic level or lower are largely ignored. Since systematic palynology is a relatively recent science, frequently less consensus of opinion has been reached in the development and application of its terminology than is the case with other areas of botany. Where it appeared necessary, new palynological terms and definitions have been adopted and certain concepts clarified. In all such cases a guiding principle has been to preserve terminology and definitions which are in wide usage as much as possible; however, in some instances, changes in terminology, definitions, or concepts were felt warranted either because new data have become available (particularly from scanning electronmicroscopy combined with study of thin-sections of the pollen wall) or because use of certain pollen characters in a phylogenetic context made a more evolutionary set of terms imperative. Pollen characters have been grouped into

seven categories, which will be treated in the following order: aperture type, pollen wall architecture, pollen-unit, polarity, symmetry, shape, and grain size.

POLLEN APERTURES

Apertures are specially delimited, generally thin-walled areas in the outer pollen wall or exine through which the pollen tube usually (but not always) emerges at the time of germination. Although most apertures seem to represent thinner areas in the exine or aperture membranes, in some pollen grains they are as thick or thicker than the exine on nonapertural areas of the same grain. Thus, it appears that the primary prerequisite for an aperture involved in pollen tube exitus is not so much a thinning of the exine, as development of a zone that is thinner *or* thicker, as compared with the rest of the pollen wall, which may act as a weak point of rupture during germination of the pollen grain. Apertures serve a second major function in that they allow for volume-change accommodations (harmomegathy) in pollen grains subjected to changes in humidity (Wodehouse, 1935; Payne, 1972). Some apertures may serve both for pollen tube exitus and harmomegathic changes, while some pollen grains have "pseudo-apertures" which appear to function solely in a harmomegathic capacity.

Numerous terms exist to describe pollen apertures. Although some of these have been proposed in papers dealing with the pollen morphology of a limited taxonomic group, such as a family, genus, etc., most aperture terms commonly in use today have been taken either from Erdtman (Erdtman, 1966; Erdtman & Vishnu-Mittre, 1956; Erdtman & Straka, 1961) or Faegri & Iversen (1964). While the aperture terminology developed by Faegri and Iversen has the advantage of simplicity, that developed by Erdtman (which has been frequently modified or changed) is more useful phylogenetically. The description of aperture types outlined in this paper is based largely on the earlier aperture terminology developed by Erdtman, although certain novelties have been introduced.

Pollen apertures may be categorized largely on the basis of their (1) number, (2) shape, (3) position, and (4) structure (i.e., whether they are simple or compound). For routine pollen identification, aperture number, shape, and structure are often all that is required. However, in a phylogenetic-evolutionary context, *position* of the aperture(s) is of paramount importance.

Aperture Number.—With respect to number of apertures, pollen appears to be best classified phylogenetically as: (1) inaperturate (without any apertures), (2) mono-aperturate (with one aperture), (3) di-aperturate (with two apertures), (4) tri-aperturate (with three apertures), or (5) poly-aperturate (with more than three apertures). Poly-aperturate pollen grains are most frequently tetra-, penta-, or hexa-aperturate (i.e., with 4, 5, or 6 apertures).

Aperture Shape.—With regard to shape (and irrespective of position), pollen grains basically may have three different types of apertures, including: (1) elongate, furrow-like apertures (colpate pollen, sensu lato), (2) round, pore-like apertures (porate pollen, sensu lato), and (3) encircling, ring- or band-like apertures (zonate pollen). Weakly defined apertures may be indicated by introduction of the syllable -oid- into the terms describing the corresponding well-developed apertures, e.g., colpoidate pollen would have poorly developed furrow-

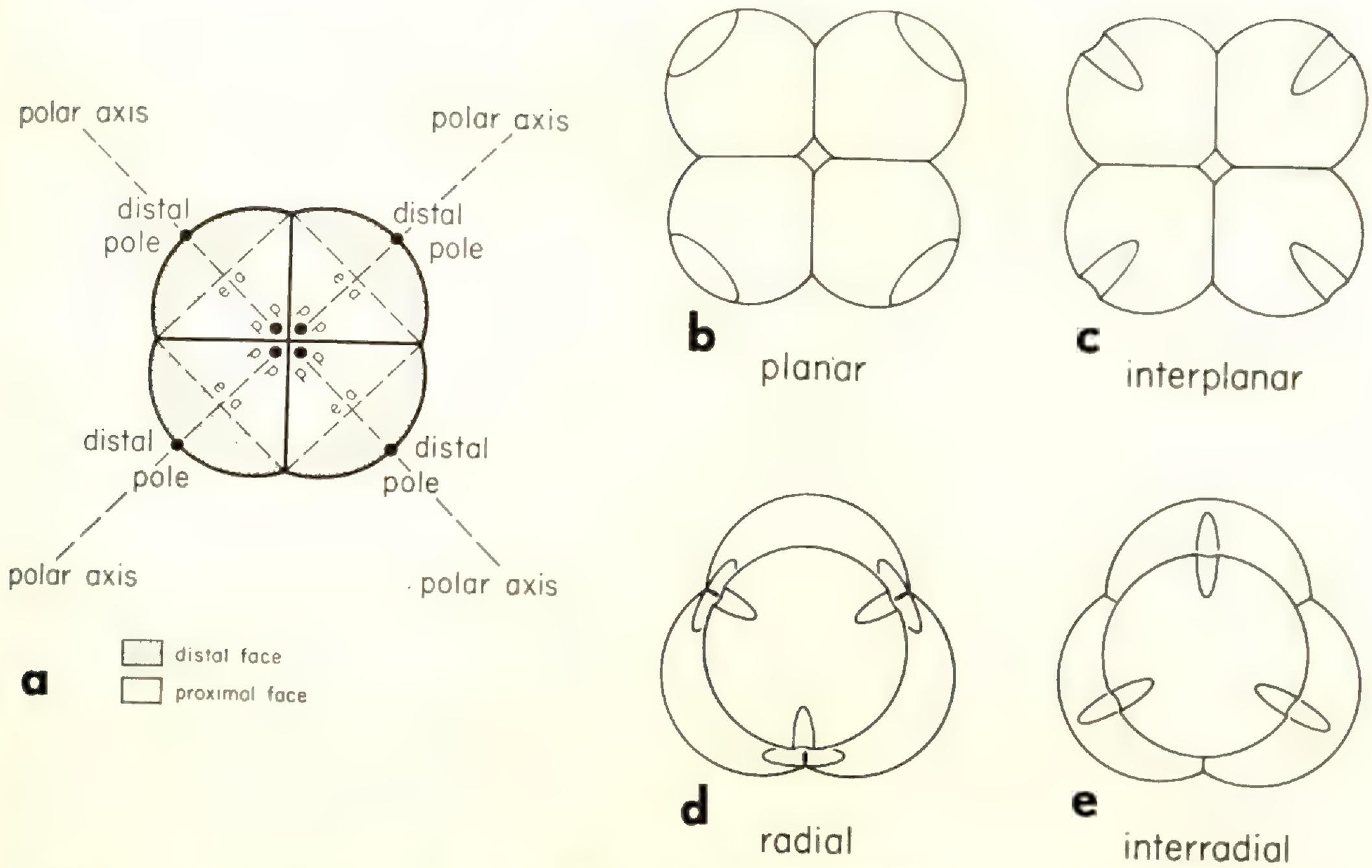

FIGURE 1. Relationships of pollen tetrads and aperture positions.—a. Diagram of a tetragonal pollen tetrad showing the polar axis, one equatorial axis (e.a.) of the equatorial plane, the distal face, the proximal face, the distal pole, and the proximal pole (p.p.) of each pollen grain in the tetrad.—b–c. Tetragonal tetrads showing placement of distal-polar, furrow-like apertures in planar and interplanar positions.—d–e. Tetrahedral tetrads showing placement of equatorial, furrow-like apertures in radial and interradial positions; top pollen grain shown in polar view with its polar axis perpendicular to the plane of the figure.

like apertures or colpoids. Pollen with one or more weakly defined, more or less irregularly shaped aperturoid areas may be described as tenuitate, the poorly defined apertural area constituting a tenuitas. In some pollen, the aperture may be covered by a thickened lid or operculum, resulting in an operculate aperture.

Aperture Position.—Although some or all members of approximately 50 families of angiosperms have mature pollen grains shed as dyads, tetrads, polyads, or other large pollen-units (cf., below), most pollen as observed at maturity within the anther locules of the stamen consists of solitary grains or monads. However, since pollen always results from meiosis of pollen mother cells (PMC's), all pollen grains are at one time or another united together as members of a meiotic pollen tetrad. This fact allows certain dimensions of even a solitary pollen grain or monad to be defined in terms of the spatial relationships of the four grains of the pollen tetrad of which it was previously a member. Individual pollen grains may thus be likened to a globe with poles and an equator (Fig. 1a). The following definitions are derived from such an analogy. The polar axis of a pollen grain is defined as the line passing through the center of the grain from the outside to the center of the pollen tetrad (or to the center of the meiotic tetrad at the time of its formation in the case of solitary grains). The equatorial plane of a pollen grain, which contains two or more equatorial axes, perpendicularly bisects the polar axis and forms the boundary (equator) between the outer distal and inner proximal faces of the grain. The distal pole of a pollen grain faces away from the meiotic

tetrad, while the proximal pole is directed inward, facing the center of the tetrad. The single most important taxonomic-phylogenetic feature of pollen apertures is that they are not located randomly upon the surface of the pollen grain, but usually have very definite placement with reference to its poles and equator. Determination of absolute pollen grain polarity (cf. below) and with it absolute aperture position (i.e., knowledge of aperture position with reference to distal versus proximal pole or with reference to elongate equatorial apertures being either perpendicular or parallel to the equator) is of special importance in determining certain aperture types (e.g., anasulcate versus catasulcate or dicolpate versus disulculate, cf. below) and hence possibly aperture homologies. The determination of absolute aperture position in species with tetrads at maturity is quite straightforward. In taxa with solitary grains, however, the correct determination of absolute aperture position may be somewhat more difficult—one must either rely on comparative studies of related taxa with permanent tetrads or study cytologically the development of immature pollen tetrads before the grains separate. In practice, moreover, one frequently relies on apparent pollen grain polarity and symmetry axes (cf. below) to infer the position of apertures.

With respect to their position, three basic types of apertures may be recognized: (1) polar apertures located at or toward the poles, (2) equatorial apertures located on or at the equator, and (3) global apertures more or less uniformly scattered over the surface of the pollen grain. Polar apertures in turn may be classified with regard to the pole upon which the aperture is located, i.e., distal-polar or ana-aperturate if the aperture is located at or toward the distal pole and proximal-polar or cata-aperturate if the aperture is at or toward the proximal pole. With regard to position, elongate or ring-like apertures may be characterized further as meridional or latitudinal. Meridional (or longitudinal) apertures have their long axis perpendicular to the equator of the pollen grain and go through both poles (or would if extended), while latitudinal (or transverse) apertures have their long axis on or parallel to the equator (i.e., perpendicular to the polar axis) and would not go through the poles even if extended. The prefixes axi-, zoni-, and pan- are used, respectively, to refer to apertures located at or toward the poles, on or at the equator, and over the entire pollen surface, while the prefixes ana- and cata- refer to polar apertures which are distal-polar or proximal-polar. The prefix zona- is used to refer to a ring- or band-like aperture.

Apertures also possess a relative tetrad position, i.e., the position of each aperture of a given pollen grain relative to the position of the apertures of the other pollen grains of the pollen tetrad of which the particular pollen grain is a

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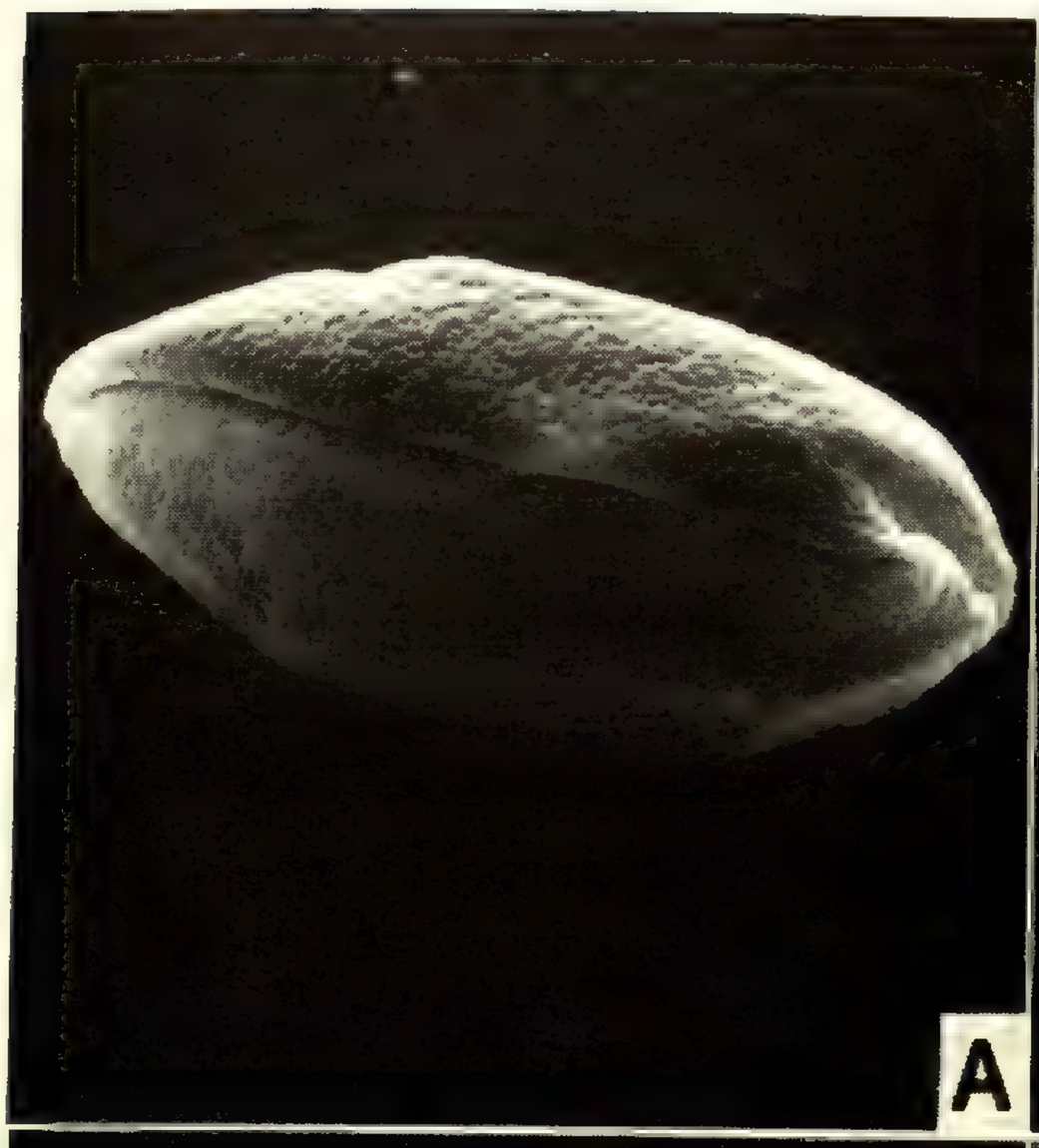
FIGURE 2. Polar and equatorial pollen apertures.—A. Anasulcate pollen; × ca. 820 (*Magnolia fraseri* Walt.; Magnoliaceae). Presumed distal-polar view.—B. Anatrichotomosulcate pollen; × ca. 820 (*Pseudoxandra coriacea* R. E. Fries; Annonaceae). Two grains of a permanent tetrahedral tetrad.—C. Anaulcerate pollen; × ca. 1340 (*Drimys confertifolia* Phil.; Winteraceae). Grains in a permanent tetrahedral tetrad.—D. Anazonasulculate pollen; × ca. 1660 (*Nymphaea amazonum* Mart. & Zucc.; Nymphaeaceae). Presumed distal-polar view.—E. Zonizonasulculate pollen; × ca. 1240 (*Nymphaea violacea* Lehm.; Nymphaeaceae).—F. Disulculate pollen; × ca. 1160 (*Calycanthus floridus* L.; Calycanthaceae). Presumed equatorial view with polar axis vertical and equatorial plane horizontal.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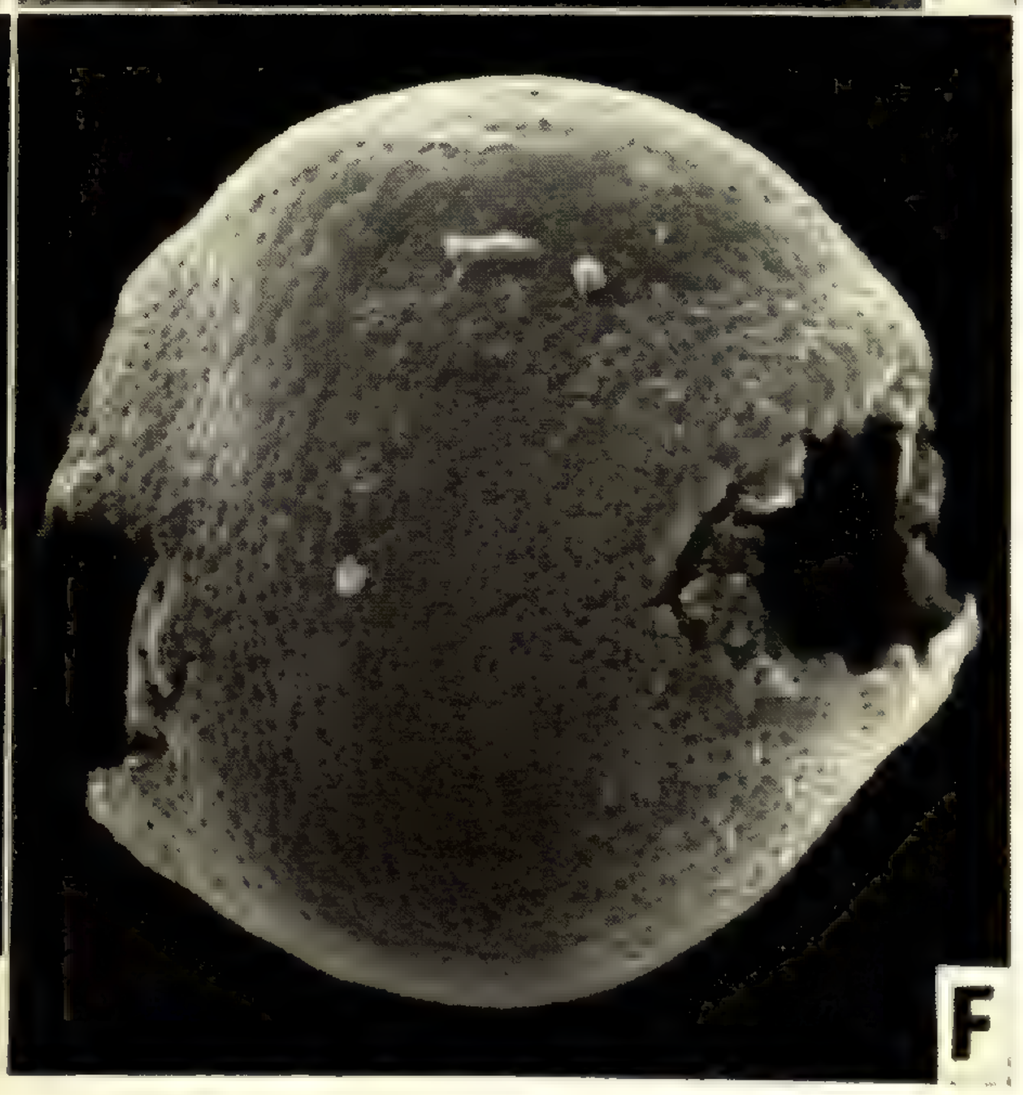
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member. Single, polar, elongate, furrow-like apertures, which most commonly occur on pollen grains in tetragonal tetrads (cf. below), are generally found in an interplanar tetrad position, i.e., with the long axis of each furrow-like aperture more or less perpendicular to the plane of the tetrad (Fig. 1c), less frequently in a planar position, i.e., with the long axis of each furrow-like aperture in the same plane as the pollen grains of the tetrad itself (Fig. 1b; Walker, 1974c). Pollen grains with three equidistant equatorial apertures, which are the most common type of angiosperm pollen grains and which generally occur in tetrahedral tetrads (cf. below), almost always have their apertures in an interradial position, i.e., the apertures meet at points where only two grains of the tetrad are in contact, in six groups of two apertures each (Fig. 1e), while such apertures very rarely occur in a radial position, i.e., the apertures meet at the points where three grains of the tetrad are in contact, in four groups of three apertures each (Fig. 1d). Arrangement of apertures in the former tetrad position has been referred to as "Fischer's rule," while arrangement in the latter position has been called "Garside's rule" (cf. Erdtman, 1969).

Polar Apertures (Axi-aperturate Pollen).—Polar aperture types include sulcate pollen with a single, polar, elongate, furrow-like aperture known as a sulcus (plural, sulci), ulcerate pollen with a single, polar, rounded, pore-like aperture known as an ulcus (plural, ulci), and axizonasulculate pollen with a single, latitudinal, ring- or band-like aperture encircling one of the poles known as an axizonasulculus (plural, axizonasulculi). If the above apertures are known to be located at or toward the distal pole (i.e., are ana-aperturate), the pollen may be described respectively as anasulcate (Fig. 2A), anaulcerate (Fig. 2C), and anazonasulculate (Fig. 2D). Pollen with corresponding proximal-polar (i.e., cata-aperturate) apertures would be catasulcate, cataulcerate, or catazonasulculate. Except for some catasulcate-cataulcerate pollen in the Annonaceae (Walker, 1971b, 1972b), all other sulcate or ulcerate angiosperm pollen appears to be distal-polar (e.g., Bailey & Swamy, 1949; Canright, 1953; Swamy, 1949; Wilson, 1964), and therefore sulcate or ulcerate apertures are probably best considered to be distally located (i.e., anasulcate or anaulcerate) unless proved otherwise. Sometimes anasulcate pollen may be three-armed or anatrichotomosulcate (Fig. 2B), or more rarely even 4-armed or tetrachotomosulcate. Sulci, trichotomosulci, and ulci all have their center located at one of the poles, while axizonasulculi run around one of the poles. All polar apertures are essentially meridional with the exception of axizonasulculate apertures which are latitudinal. Axi-aperturate pollen is almost always mono-aperturate.

Equatorial Apertures (Zoni-aperturate Pollen).—Equatorial aperture types

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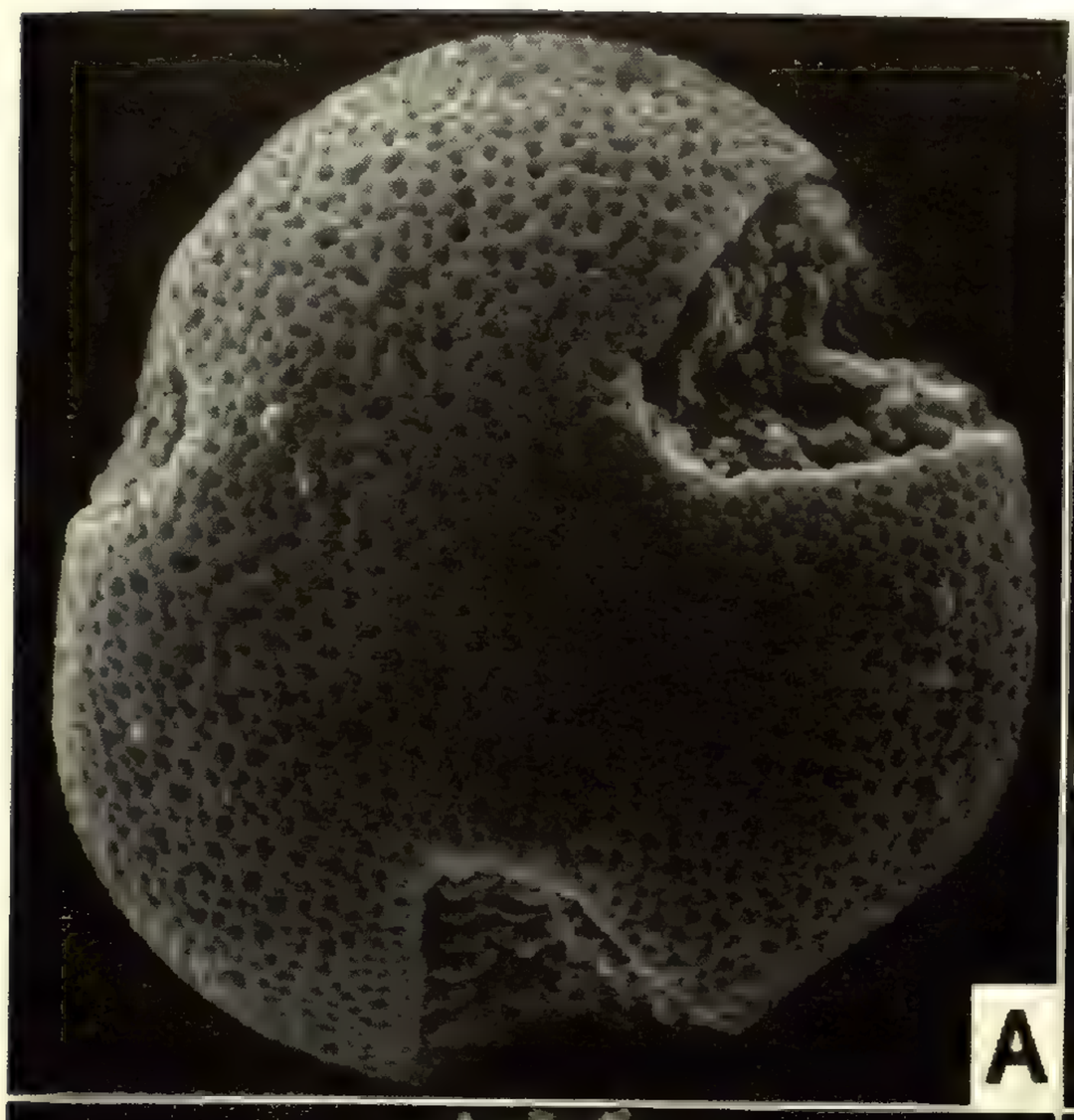
FIGURE 3. Equatorial and global pollen apertures.—A. Tricolpate pollen; × ca. 1890 (*Euptelea pleiosperma* Hook.f. & Thomas; Eupteleaceae). Polar view.—B. Triporate pollen; × ca. 900 (*Euplassa inaequalis* (Pohl) Engl.; Proteaceae). Polar view.—C. Syntricolpate pollen; × ca. 2240 (*Schisandra grandiflora* (Wall.) Hook.f. & Th.; Schisandraceae). Presumed distal-polar view.—D. Tricolporate pollen; × ca. 3350 (*Limacia sagittata* Oliv.; Menispermaceae). Equatorial view.—E. Rugate pollen; × ca. 2530 (*Euptelea polyandra* Sieb. & Zucc.; Eupteleaceae).—F. Forate pollen; × ca. 2800 (*Trimenia papuana* Ridl.; Trimeniaceae).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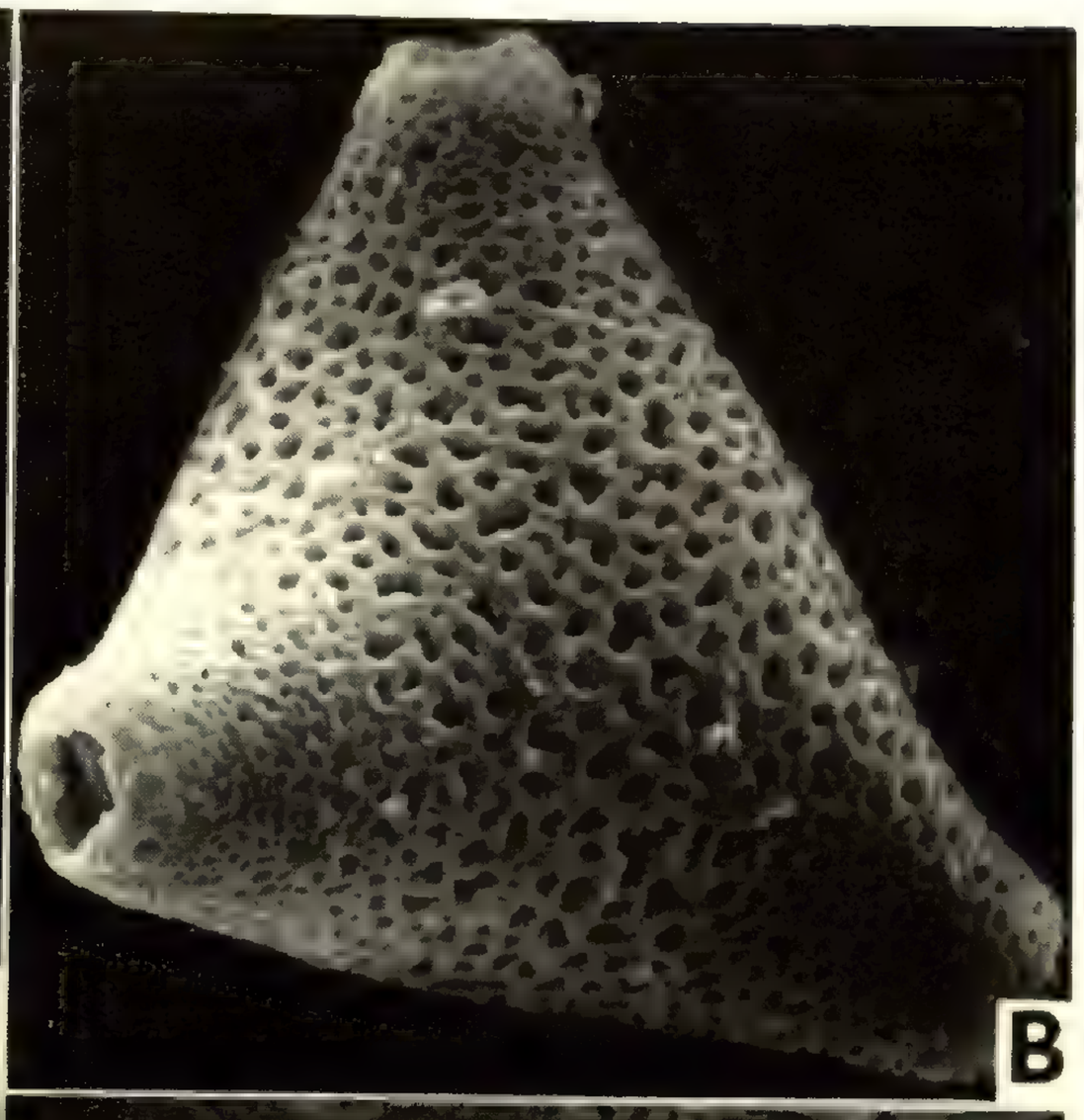
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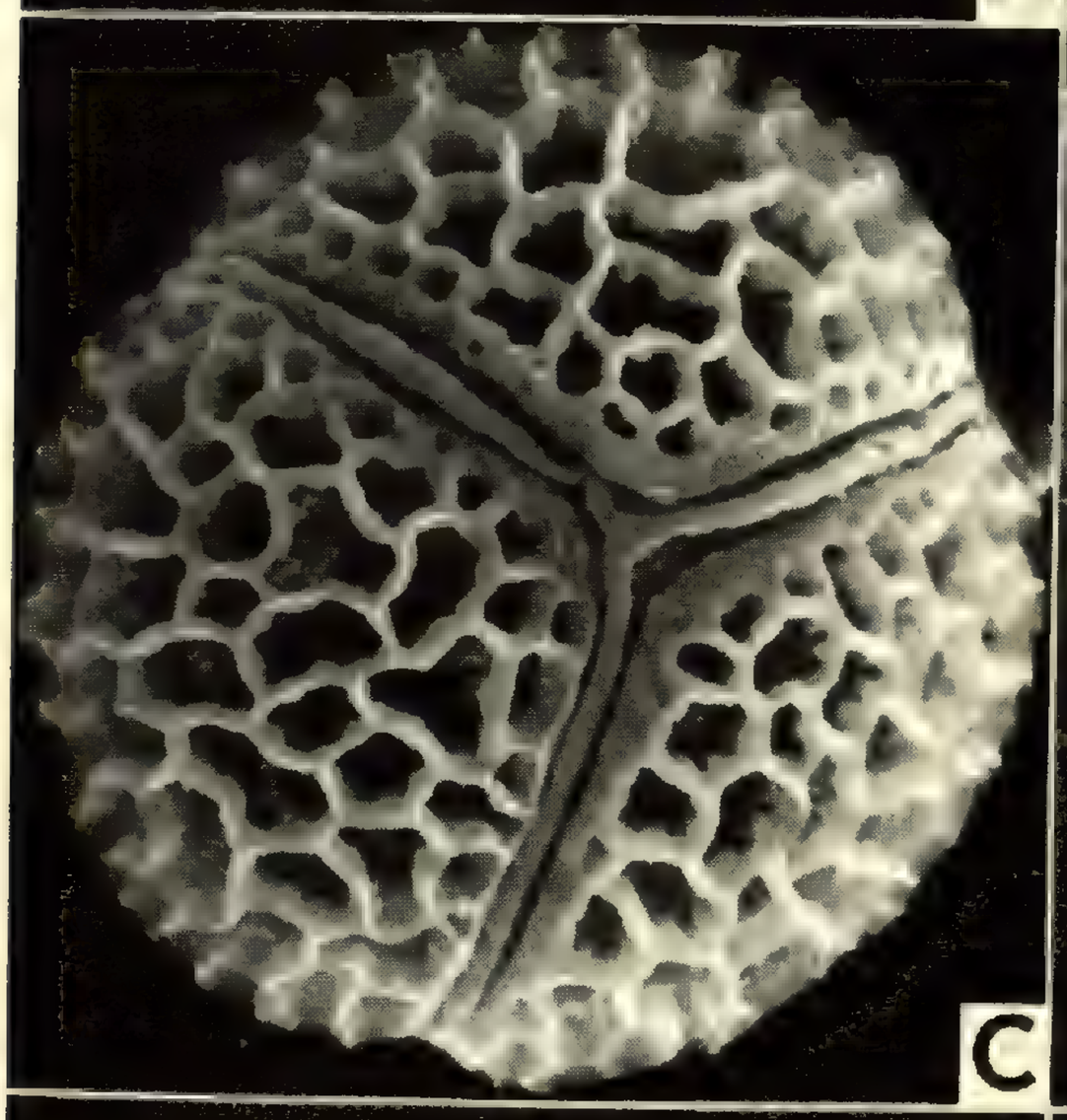
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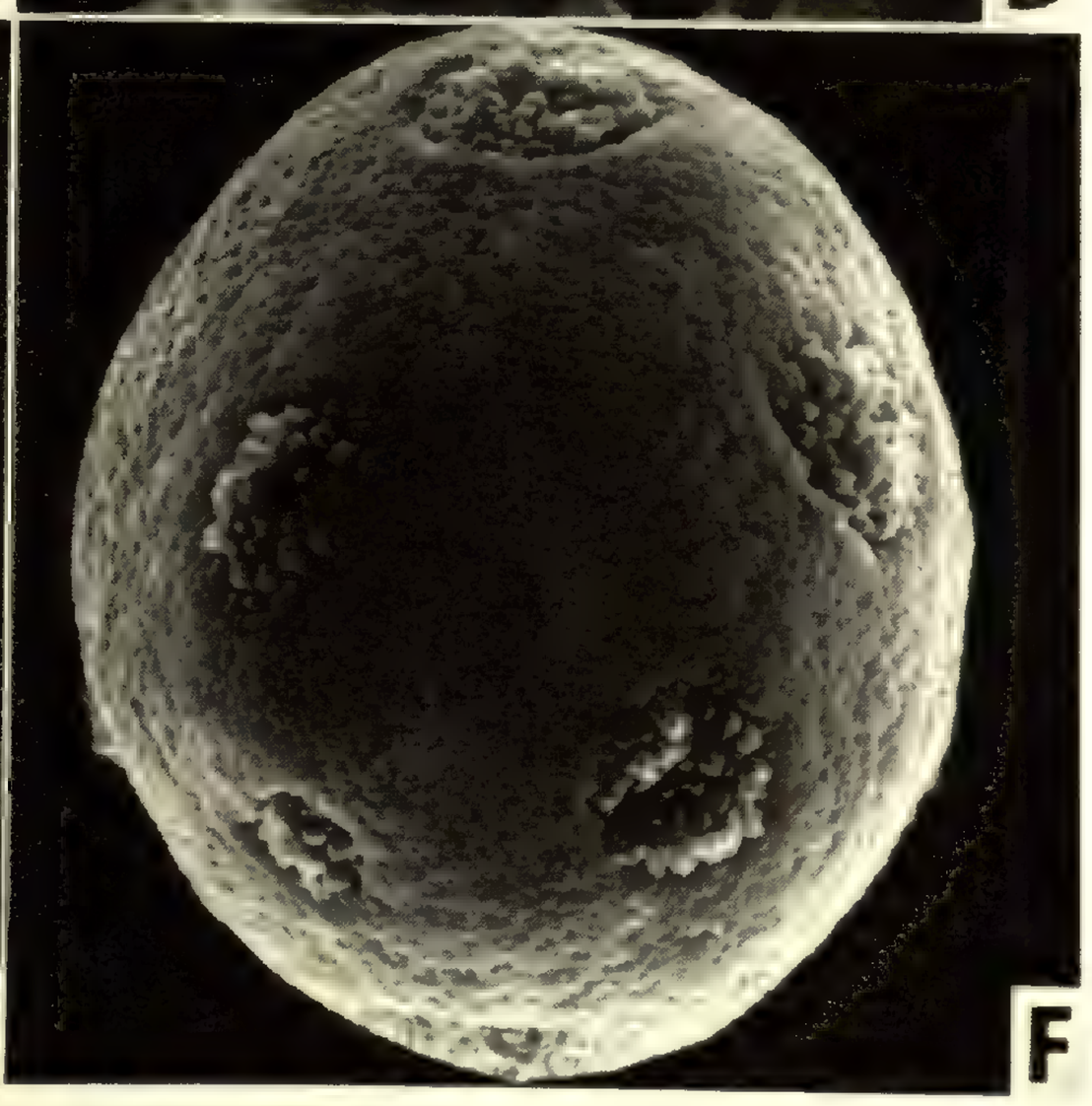
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include colpate pollen, sensu stricto,[5] (Fig. 3A) with meridional, elongate, furrow-like apertures located equidistantly at the equator and normally bisected by the equatorial plane known as colpi (singular, colpus), porate pollen, sensu stricto,[5] (Fig. 3B) with round, pore-like apertures located equidistantly on the equator known as pores (singular, pore), sulculate pollen (Fig. 2F) with latitudinal, elongate, furrow-like apertures located equidistantly on the equator known as sulculi (singular, sulculus), and zonizonasulculate pollen (Fig. 2E) with a latitudinal, ring- or band-like, encircling aperture running around the equator known as a zonizonasulculus (plural, zonizonasulculi). Pollen with equatorial, rounded apertures derived from sulculi (i.e., the pore-like apertures are latitudinal-derived) may be described as ulculate, with the pore-like apertures being ulculi (singular, ulculus). The pores in porate pollen, on the other hand, are not derived through shortening of previously existing sulculi, but are basically meridionally derived via shortening of colpi instead of sulculi. If a pollen grain should have an encircling, ring-like aperture that is latitudinal and clearly not meridional, but no more is known about its exact position (i.e., whether it is axizonasulculate, anazonasulculate, catazonasulculate, or zonizonasulculate), it should be described simply as zonasulculate. A pollen grain with a single, encircling, ring- or band-like aperture which is meridional rather than latitudinal may be described as zonasulcate, with the aperture being a zonasulcus (plural, zonasulci). Zoni-aperturate pollen, unlike axi-aperturate pollen, usually has more than one aperture (except for zonizonasulculate and zonasulcate pollen which is mono-aperturate). Sulculate-ulculate pollen appears to be almost always di-aperturate (i.e., disulculate, diulculate), while colpate and porate pollen is usually tri-aperturate (i.e., tricolpate, triporate), less frequently di-aperturate (e.g., dicolpate, diporate). Although much less frequent than tricolpate, colpate pollen may also be 4-colpate, 5-colpate, or 6-colpate, more rarely 7–12-colpate or greater than 12-colpate. In some colpate pollen, all or some of the colpi may be fused at one or both poles resulting in different types of syncolpate pollen grains (Fig. 3C).

Global Apertures (Pan-aperturate Pollen).—Global apertures may be elongate and furrow-like (rugae; singular, ruga) resulting in rugate pollen (Fig. 3E), or round and pore-like (foramina; singular, foramen) resulting in forate pollen grains (Fig. 3F). Although rugate pollen may have six or less apertures, forate pollen usually has more than six apertures and frequently more than 12 apertures.

Miscellaneous Aperture Types.—There are a number of miscellaneous aperture types which are frequently difficult to categorize, e.g., pollen of the rosaceous genera *Grielum* and *Neurada* (cf. Erdtman, 1966) which appears to possess 3-armed apertures at both poles (which may have originated from bipolarly fused tricolpate pollen that subsequently lost connecting parts of the colpi in the region of the equator). Pollen of *Commelinantia* (Commelinaceae) exemplifies another distinctive aperture type (cf. Rowley & Dahl, 1962). Another rare

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[5] The terms colpate and porate have been used by a number of authors in a broad sense to refer to any apertures irrespective of position which are respectively elongate and furrow-like or round and pore-like. Here and elsewhere in this paper, unless otherwise noted, these terms are used in the more restricted sense to refer solely to meridionally elongate or meridionally derived rounded apertures which are equatorially located.

aperture type occurs in the "3-ulcerate" pollen of some monocotyledons (e.g., palms) which have three, equidistant, pore-like apertures situated around one pole that may have been derived from a trichotomosulcus. A more frequently met miscellaneous aperture type is represented by spiraperturate pollen grains which have a number of elongated, furrow-like apertures that are spirally arranged. Also, apertures infrequently may be borne on more or less rounded, protruding, dome-like areas, thus producing aspidote pollen. If a chamber is formed in such pollen grains between an outer and inner aperture opening, it is known as an atrium (plural, atria). Pollen grains with locally thickened areas of the exine which extend in sweeping curves from aperture to aperture (arci; singular, arcus) may be described as arcuate.

Aperture Structure.—Pollen apertures may be simple or compound. Simple apertures have more or less uniform aperture membranes, while compound or orate apertures (Fig. 3D) possess specially delimited areas of the aperture membrane known as ora (singular, os). Most compound apertures are mono-orate with one os per aperture; however, diorate pollen with two ora per aperture does occur, although rather infrequently. Ora are usually, although not always, more or less rounded. Extended or elongate ora may be either transversely (latitudinally) elongated and lalongate or longitudinally (meridionally) elongated and lolongate. The following aperture types are exclusively simple: sulcate, trichotomosulcate, zonasulcate, ulcerate, sulculate, ulculate, and zonasulculate. Rugate and forate pollen may have either simple or compound apertures. Colpate and porate pollen grains may have simple or compound apertures, with compound apertures being the more frequent. Compound apertures are designated by introducing the syllable -or- into the terms describing the corresponding simple apertures. Thus, colpate, porate, rugate, and forate pollen with compound apertures would be called colporate, pororate, rugorate, and fororate. Of these, the most common type of compound-aperturate pollen is represented by colporate pollen grains, which have pore-like structures in the center of the colpi. Colporoidate pollen would have well developed colpi with weakly developed ora (oroids), while colpoidorate pollen would have weakly developed colpi (colpoids) with well developed ora. Similarly, pororoidate pollen would have well developed pores with the ora weakly developed, while poroidorate pollen has weakly developed pores (poroids) with well developed ora. The main characteristics of the basic types of apertures found in angiosperm pollen are summarized in Table 1.

Evolution of Pollen Aperture Types.—The evolution of apertures in pollen grains was one of the major advances of seed plants, and aperture type (along with the pollen wall) constitutes one of the most important phylogenetic pollen characters. The spores of pteridophytes, in the strict sense, do not possess apertures; however, their spores do have analogous, weakened areas on the proximal pole called tetrad scars by which they often open. These scars may be either trilete (triradiate or Y-shaped) or monolete (straight). It was in gymnospermous plants that the first true apertures evolved. Certain fossil gymnosperm pollen grains (e.g., the pollen grains of some pteridosperms) still retain a trilete tetrad scar on the proximal face which is homologous to the tetrad scar of

TABLE 1. Main characteristics of basic angiosperm pollen aperture types.

Aperture Shape	Aperture Position	Number of Apertures	Aperture Type[a]
Furrow-like	Unknown	1–many	Colpate, sensu lato
	Polar (axi-aperturate)	1	(Mono)Sulcate
	Distal-polar (ana-aperturate)	1	Anasulcate[b]
	Proximal-polar (cata-aperturate)	1	Catasulcate
	Equatorial (zoni-aperturate)		
	Meridional (longitudinal)	2–many	Colpate, sensu stricto
	Latitudinal	2	(Di)Sulculate
	Global (pan-aperturate)	4–many	Rugate
Pore-like	Unknown	1–many	Porate, sensu lato
	Polar (axi-aperturate)	1	(Mono)Ulcerate
	Distal-polar (ana-aperturate)	1	Anaulcerate
	Proximal-polar (cata-aperturate)	1	Cataulcerate
	Equatorial (zoni-aperturate)		
	Meridional-derived	2–many	Porate, sensu stricto
	Latitudinal-derived	2	(Di)Ulculate
	Global (pan-aperturate)	4–many	Forate
Ring-like	Unknown	1	Zonate
	Polar (axi-aperturate)	1	Axizonasulculate
	Distal-polar (ana-aperturate)	1	Anazonasulculate
	Proximal-polar (cata-aperturate)	1	Catazonasulculate
	Equatorial (zoni-aperturate)		
	Meridional	1	Zonasulcate
	Latitudinal	1	Zonizonasulcate[c]

[a] Sulcate, trichotomosulcate, ulcerate, sulculate, ulculate, zonasulculate, and zonasulcate apertures are always simple. Colpate, porate, rugate, and forate apertures may be simple or compound.

[b] Anasulcate pollen grains may occasionally be 3-armed or anatrichotomosulcate, more rarely 4-armed or tetrachotomosulcate.

[c] A ring-like aperture that is clearly latitudinal and not meridional (but unspecified as to being around one of the poles or the equator) may be described simply as zonasulculate.

pteridophyte spores (Wodehouse, 1935; Chaloner, 1970). The first true apertures, however, evolved at the distal pole (facing outward in the meiotic tetrad) and were furrow-like (sulcate). With reference to angiosperm pollen, two basic aperture types are generally recognized (Fischer, 1890; Wodehouse, 1935; Kuprianova, 1967, 1969): *monosulcate* (*monocolpate*, sensu lato, of some authors)—with a single, furrow-like aperture located at one of the poles (usually the distal), and *tricolpate*—with three, equidistant, furrow-like apertures that are perpendicular to the equator (i.e., meridional). However, since it is clear that in at least two different families of the Magnoliidae (Chloranthaceae, Aristolochiaceae), monosulcate pollen evolved into polycolpate (or polyporate) pollen, i.e., pollen with more than three colpi or pores, via an inaperturate intermediary form without going through a tricolpate stage (cf. Walker, 1974c), a more general distinction in terms of *evolutionary grade* would be between sulcate and simply colpate pollen. Colpate pollen is essentially restricted to dicotyledonous angiosperms,

while sulcate pollen is found in gymnosperms, the monocots, and some ranalean dicots.

Angiosperm pollen is thus divided into two fundamentally different types—that which is *monosulcate or monosulcate-derived* versus pollen which is *tricolpate or tricolpate-derived*, depending on whether their ancestral forms are believed to have been monosulcate or tricolpate. Although in a sense all angiosperm pollen other than monosulcate pollen itself is "monosulcate-derived," tricolpate and tricolpate-derived pollen is recognized as distinct from other "monosulcate-derived pollen" because tricolpate pollen (and its derivative forms) is the main type of pollen found in most dicotyledons, is essentially restricted to dicotyledonous angiosperms, and has served as the basis for a radiation of "tricolpate-derived" aperture types. Monosulcate-derived pollen also differs from tricolpate-derived pollen, other than in aperture number and position (monosulcate-derived pollen usually, but certainly not always, having one polar aperture, while tricolpate-derived pollen usually has three equatorial apertures), in that it always has simple apertures, while most tricolpate-derived pollen has compound apertures. Monosulcate-derived apertures include polar aperture types such as found in trichotomosulcate, ulcerate, and axizonasulculate pollen, as well as some equatorial aperture types such as found in sulculate, ulculate, zonizonasulculate, and zonasulcate pollen. Tricolpate-derived apertures (e.g., tricolporate, triporate, etc.), on the other hand, are almost always equatorial. Global apertures may be either monosulcate- or tricolpate-derived (e.g., forate pollen grains in the monocotyledonous family Alismataceae and the non-magnoliid dicot family Malvaceae), although rugate pollen appears to be restricted to the non-magnoliid dicots, i.e., is tricolpate-derived. Inaperturate pollen likewise may be either monosulcate- or tricolpate-derived. The polycolpate/polyporate pollen found in the Chloranthaceae and Aristolochiaceae must be considered unique in being clearly monosulcate-derived; all other colpate pollen in dicotyledonous angiosperms appears to be tricolpate or tricolpate-derived. By contrast, monosulcate or monosulcate-derived pollen is unknown among non-magnoliid dicotyledons, being restricted, as previously indicated, to some ranalean dicots, the monocotyledons, and gymnosperms.

A single, furrow-like aperture located at the distal pole of the pollen grain (an anasulcus) is undoubtedly the primitive (ancestral) aperture type in the angiosperms (Walker, 1974c). This is borne out by several lines of evidence. First, anasulcate pollen is found in, and is widespread among, extant and fossil gymnosperms. Secondly, within the angiosperms themselves, anasulcate pollen is restricted to the otherwise most primitive subclass of dicotyledons, the Magnoliidae, and to the monocots, the bulk of dicotyledonous angiosperms having tricolpate or tricolpate-derived aperture types. Also, anasulcate pollen occurs in what are believed to be the more primitive members *within* the subclass Magnoliidae. Finally, monosulcate pollen has been shown to precede other angiospermous aperture types in the fossil record (Doyle, 1969; Muller, 1970).

Within primitive ranalean dicots (subclass Magnoliidae), anasulcate pollen has given rise more or less directly to the following aperture types (Fig. 4; Walker, 1974c): anatrichotomosulcate, zonasulculate, anaulcerate, catasulcate-

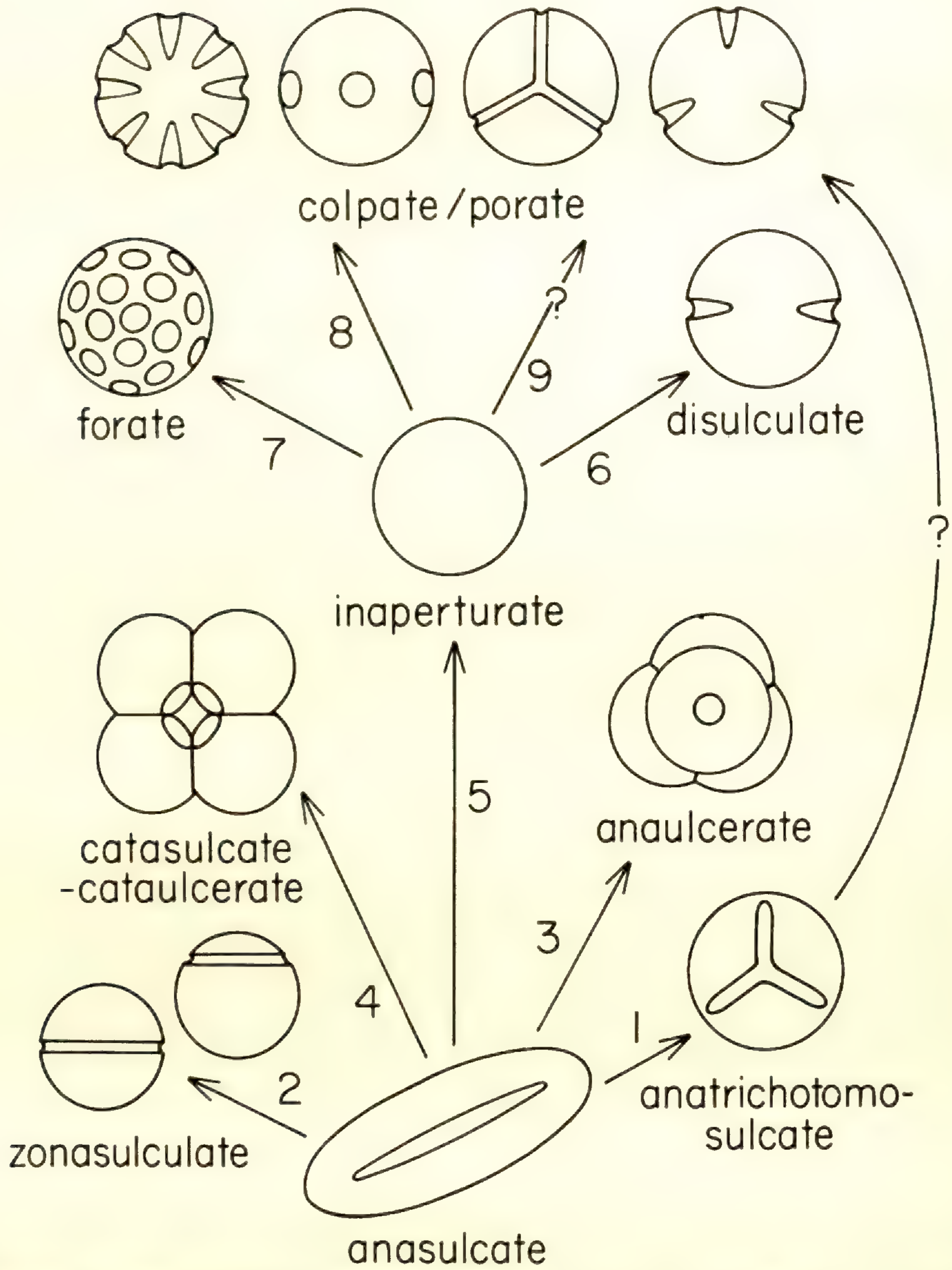

FIGURE 4. Major evolutionary trends in pollen apertures of magnoliid dicots. Anasulcate, anatrichotomosulcate, anaulcerate, polycolpate, syntricolpate, and tricolpate pollen shown in polar view; zonasulculate, catasulcate-cataulcerate, disulculate, and triporate pollen shown in equatorial view. See text for discussion.

cataulcerate, and inaperturate (and thence to disulculate and forate pollen). Evidence from extant primitive angiosperms suggests that inaperturate, not trichotomosulcate pollen (cf. Straka, 1963; Wilson, 1964), was the ancestral pollen type which gave rise to the uniquely angiospermous (dicotyledonous) colpate pollen aperture. From the basic tricolpate form of this colpate pollen the diversity of non-magnoliid aperture types such as 5-colpate, 6-colpate, porate, colporate, pororate, rugate, forate, etc. appear to have evolved.

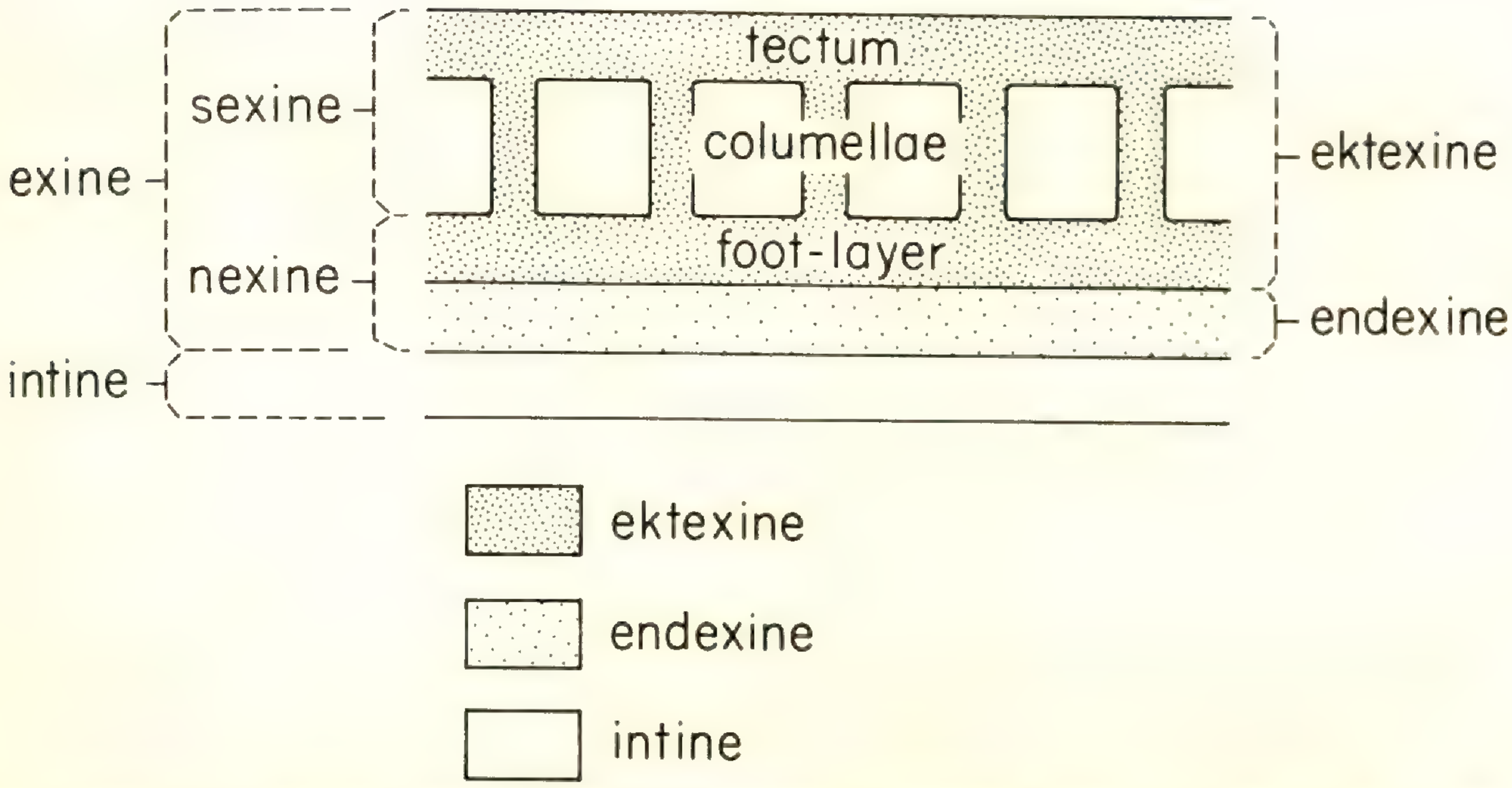

FIGURE 5. Pollen wall stratification as observed in a typical angiosperm pollen grain. This particular diagram represents a cross-section in a nonapertural area of a tectate-imperforate, non-acetolyzed pollen grain that has endexine and a foot-layer.

POLLEN WALL ARCHITECTURE

The nature of the pollen wall itself provides a multitude of phylogenetically important characters. However, probably no other palynological character has been responsible for so much terminological confusion as pollen wall morphology (cf. Wittmann & Walker, 1965; Van Campo et al., 1967; Manten, 1970; Walker, 1974b). Pollen wall architecture is here proposed to encompass all aspects of pollen wall morphology, i.e., internal structural components as well as external surface elements, and is specifically created as a broad term to include pollen wall stratification as well as exine structure and sculpturing.

Pollen Wall Stratification.—Pollen wall stratification refers to the various layers (strata) present in the pollen wall, as observed morphologically, chemically, and/or developmentally. The pollen wall of most angiosperm pollen grains (Fig. 5) consists of two fundamentally different layers: an inner, more or less cellulosic layer (the intine) which is usually destroyed upon acetolysis (cf. Faegri & Iversen, 1964); and an outer, acetolysis-resistant layer (the exine), which is composed of oxidative polymers of carotenoids and/or carotenoid esters known as sporopollenin (Shaw, 1971). However, since most modern pollen is prepared for study by acetolysis and the intine is lacking in fossil pollen, study of the pollen wall usually consists of the study of the exine.

Exine Stratification.—The exine of acetolyzed angiosperm pollen grains as observed in the light microscope (Fig. 5) typically consists of two layers: an inner, basal layer or nexine ("nonsculptured exine"); and an outer layer or sexine ("sculptured exine"). In angiosperms, a "complete" sexine is two-layered and consists of internal, up-right, rod-like elements known as columellae (bacula) covered by a roof-like layer or tectum. In fact, the presence of a middle layer of distinct, well-defined columellae (i.e., pollen tectate), rather than an irregular spongy layer (i.e., pollen alveolate), appears to be one of the main features in

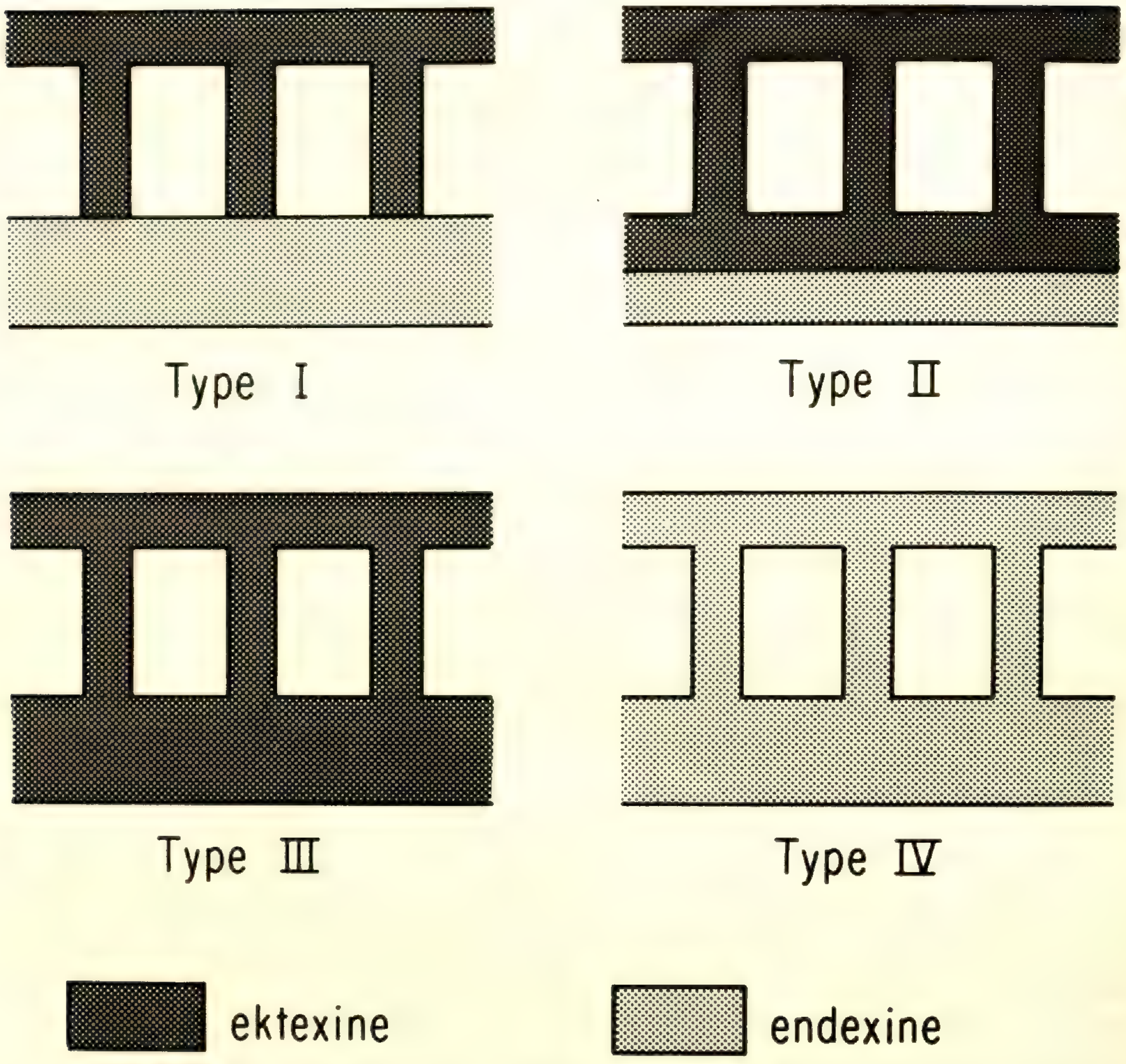

FIGURE 6. Exine stratification types. Diagrams represent cross-sections in nonapertural areas of tectate-imperforate, acetolyzed pollen grains. Type I exine is ektexinous-endexinous with no foot-layer. Type II exine is ektexinous-endexinous with a foot-layer. Type III exine is entirely ektexinous. Type IV exine is entirely endexinous.

which angiosperm exines differ in general from those of gymnosperms (Van Campo, 1971).

By proper staining and light microscopy (Faegri, 1956) or more readily with transmission electron microscopy (Larson et al., 1962; Larson, 1964), the exine in a number of angiosperms has been shown to be chemically differentiated into two distinct layers (which are also developmentally correlated), the outer such layer being called the ektexine and the inner the endexine (Fig. 5). Distribution of the chemically-developmentally defined ektexine-endexine with reference to the morphologically observed sexine-nexine permits envisionment of four basic exine stratification types (Fig. 6). In some pollen the ektexine may be equivalent to the sexine (with the endexine corresponding to the nexine), i.e., the nexine is entirely endexinous (exine stratification type I). However, in many taxa an outer layer of the nexine proves to be chemically (and developmentally) similar

to the sexine (columellae and tectum, if present) when examined with the transmission electron microscope or the light microscope if the proper staining has been used (e.g., Faegri, 1956; Leffingwell, Larson & Valencia, 1970). Such an outer zone of the nexine which is chemically like the sexine is called the foot-layer (pedium, sole, nexine-1) (Fig. 5), and in pollen grains of this kind the endexine corresponds only to an inner layer of the nexine (called nexine-2 by some authors), not the entire nexine, while the ektexine includes the sexine plus foot-layer, i.e., the nexine is composed of endexine and an outer ektexinous foot-layer (exine stratification type II). Occasionally the endexine itself may be further subdivided into two chemically different layers (Walker & Skvarla, unpublished). In other pollen the exine appears to be undifferentiated into chemically distinct layers; such chemically homogeneous exine may represent ektexine exclusively and grains of this type lack an endexine, i.e., the nexine is entirely ektexinous (exine stratification type III), or the exine may be essentially endexinous with little or no ektexine (exine stratification type IV). It should be stressed that normally the amount of ektexine to endexine differs in apertural versus nonapertural areas of the exine of a given pollen grain. In many species the aperture membrane appears to be made up solely of endexine or of endexine and greatly reduced ektexine, the latter being otherwise well-developed in the nonapertural areas of the exine. In some pollen by contrast, the endexine may be extremely thick beneath the apertural area of the exine, while much thinner or even lacking entirely under the rest of the exine. Although the exine as a whole is usually acetolysis-resistant, endexine appears to be less resistant to acetolysis than ektexine. This is probably the reason that the largely endexinous aperture membranes of pollen grains are frequently found broken in pollen that has been subjected to acetolysis (cf. Figs. 2B, 2C, 2F). In some morphologically inaperturate pollen grains (which commonly may not be acetolysis-resistant), the entire pollen surface may be largely endexinous and the whole pollen grain may actually correspond to the aperture membrane of a normal pollen grain (cf. Skvarla & Rowley, 1970). Finally, the intine itself frequently exhibits pronounced thickening below the aperture regions; such thickening of the intine is known as an oncus (plural, onci).

A fundamental concept relating to the pollen wall (in a stricter sense, the pollen exine) is the difference between internal structure and external sculpturing. In the "complete" sexine described above (cf. Fig. 5), the internal, rod-like columellae constitute *structure*, while any external elements located upon the tectum, such as spines, granules, etc., constitute *sculpturing*. Thus, a basic distinction is made in such pollen between internal *infratectal*[6] structural components and external *supratectal* sculpturing elements. As previously pointed out (Walker, 1971d), the most important palynological difference between the light and the scanning electron microscope is that the former instrument shows both structure and sculpturing in such "complete" or tectate pollen grains due to the penetration of light-waves (photons) and the ability of the light microscope to produce optical sections, while the scanning electron microscope with its less penetrating electrons shows only sculpturing.

[6] Infratectal structural components are located below the tectum (between it and the nexine); entities within the tectum itself would be described as intratectal.

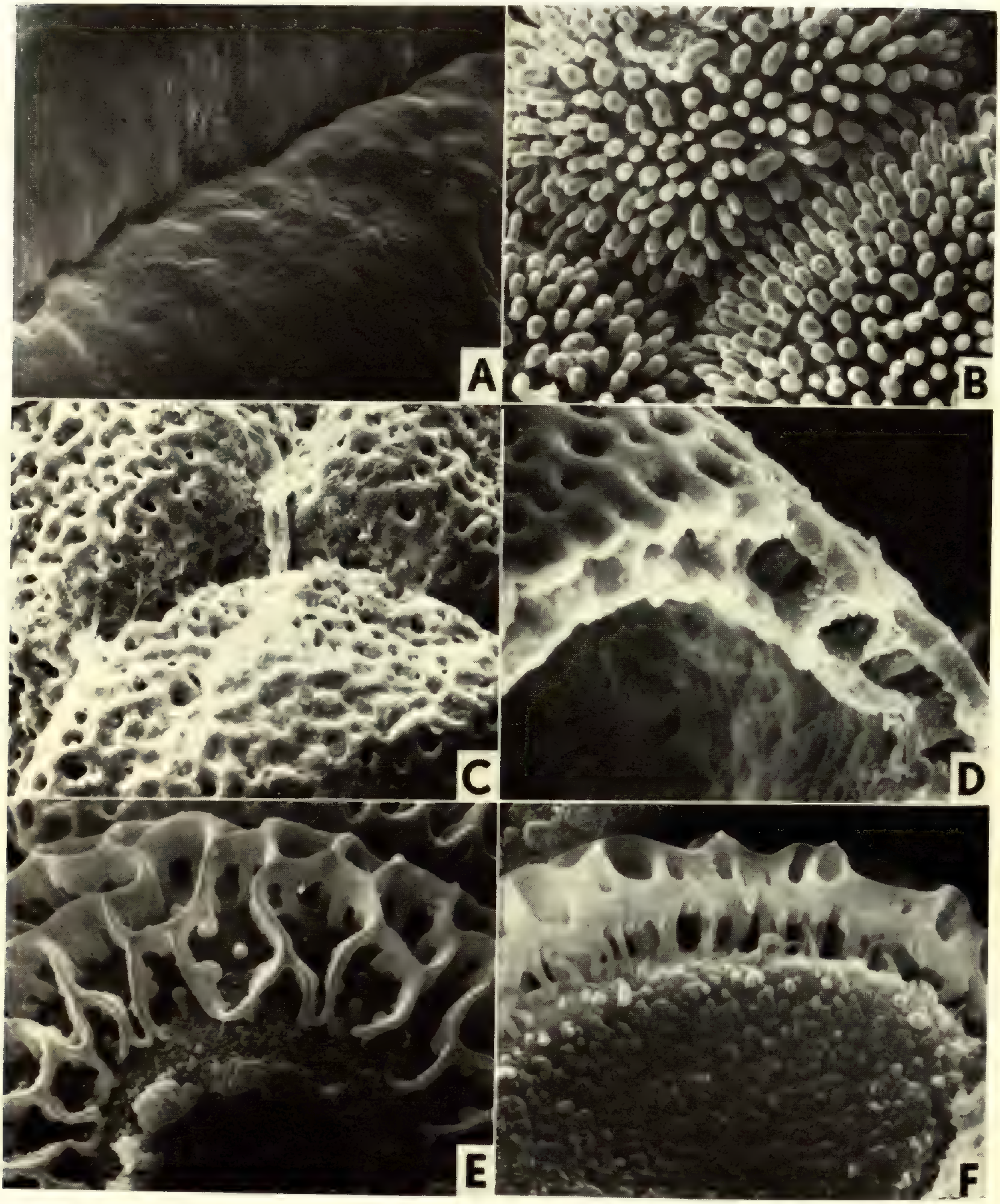

FIGURE 7. Basic angiosperm exine structure types.—A. Tectate-imperforate pollen (*Dialyanthera acuminata* Standl.; Myristicaceae). Surface view; × ca. 3450.—B. Intectate pollen (*Trigynaea caudata* (R. E. Fries) R. E. Fries; Annonaceae). Partial surface view of a polyad; × ca. 1360.—C–D. Tectate-perforate pollen (*Asimina pygmaea* (Bartr.) Dunal; Annonaceae). —C. Partial surface view of a tetrad; × ca. 1500.—D. More or less cross-sectional view; × ca. 3250.—E–F. Semitectate pollen (*Drimys confertifolia* Phil.; Winteraceae).—E. Partial surface view of two pollen grains of a permanent tetrad; hole at bottom is part of ulcerate aperture; × ca. 3500.—F. More or less cross-sectional view; × ca. 3400.

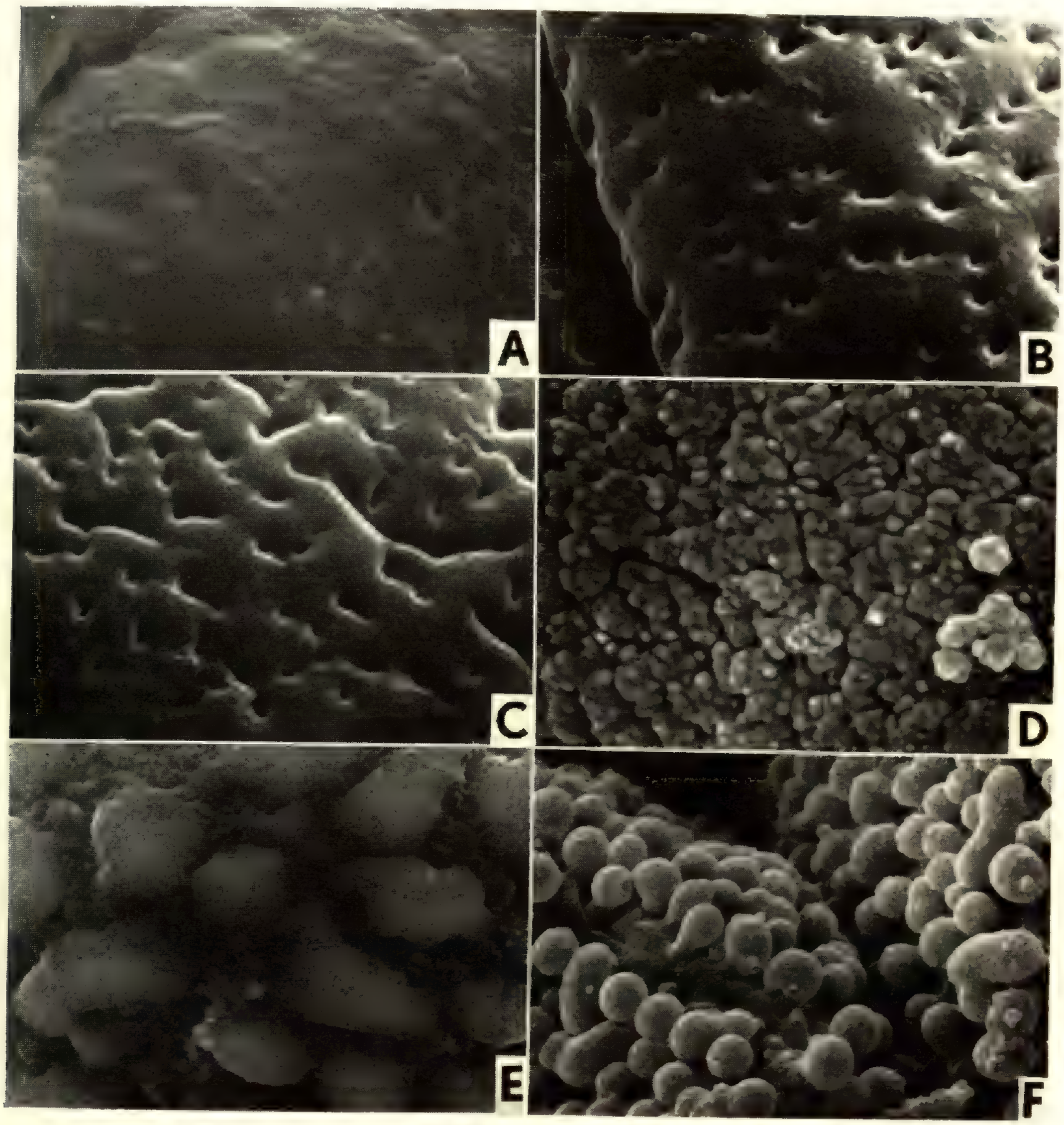

FIGURE 8. Exine sculpturing types.—A. Psilate pollen; × ca. 5000 (*Dialyanthera acuminata* Standl.; Myristicaceae).—B. Foveolate pollen; × ca. 10,000 (*Magnolia fraseri* Walt.; Magnoliaceae).—C. Fossulate pollen; × ca. 10,000 (*Pseudoxandra coriacea* R. E. Fries; Annonaceae). Foveolae present also.—D. Scabrate pollen; × ca. 8300 (*Capsicodendron dinisii* (Schw.) Occh.; Canellaceae).—E. Verrucate pollen; × ca. 4000 (*Orophea luzonensis* Merr. = *Pseuduvaria* sp.; Annonaceae).—F. Gemmate pollen; × ca. 4300 (*Ophrypetalum odoratum* Diels; Annonaceae).

Exine Structure.—Pollen of angiosperms may be divided into three basic exine structure types (Fig. 7)—tectate, semitectate, and intectate. The "complete" exine which consists of nexine, columellae, and a roof-like tectum is described as tectate, the columellae and tectum constituting the sexine in such pollen. Tectate pollen grains may be further categorized as either tectate-imperforate (without any holes in the tectum, i.e., tectal perforations) or tectate-perforate (with small holes or tectal perforations). In tectate grains, as mentioned above, the possibility exists for elements to be formed upon the roof or tectum, which then constitute the

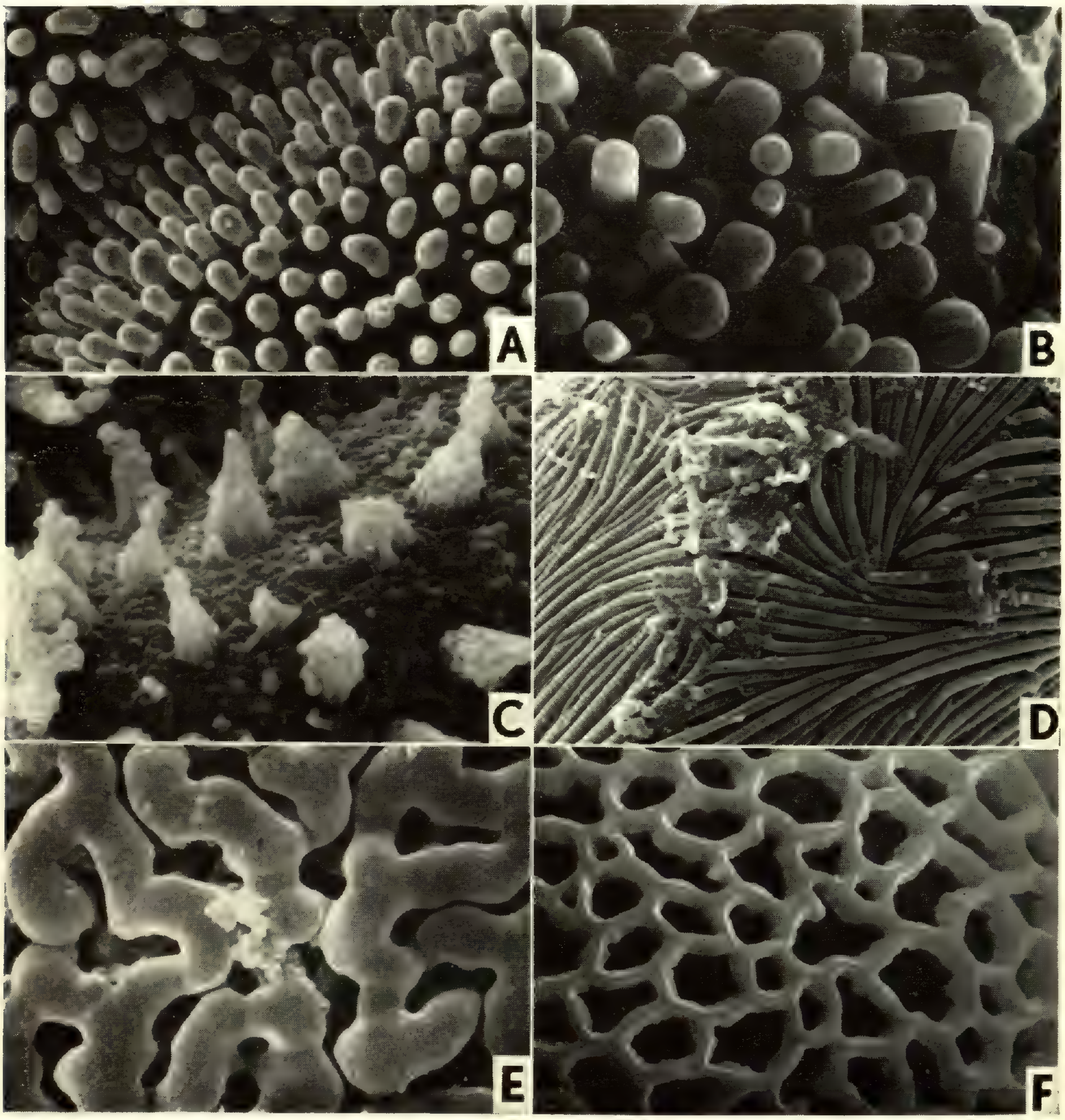

FIGURE 9. Exine sculpturing types.—A. Baculate pollen; × ca. 2000 (*Trigynaea caudata* (R. E. Fries) R. E. Fries; Annonaceae).—B. Pilate pollen; × ca. 7000 (*Nymphaea candida* J. & C. Presl; Nymphaeaceae). Bacula present also.—C. Echinate pollen; × ca. 7400 (*Peumus boldus* Mol.; Monimiaceae).—D. Striate pollen; × ca. 3800 (*Cabomba caroliniana* Gray; Cabombaceae).—E. Rugulate pollen; × ca. 6500 (*Nelumbo lutea* (Willd.) Pers.; Nelumbonaceae).—F. Reticulate pollen; × ca. 4380 (*Saruma henryi* Oliv.; Aristolochiaceae).

sculpturing. Structure in tectate grains is formed by the infratectal columellae which are enclosed by the tectum. Should the tectal perforations in a tectate-perforate exine enlarge so that their diameter becomes greater than the breadth of the pollen wall between them, an open network or reticulum may result composed of the remains of the once complete tectum either held up by otherwise free columellae or lacking columellae, which would constitute the sexine. Such pollen is described as semitectate. In semitectate, reticulate pollen the tectal perforations become spaces or lumina and the walls which make up the reticulum are known as muri. Further, should the tectum be lost entirely and only free, exposed

columellae (or their modified but homologous forms) remain as the sexine, the pollen would be described as intectate. Surface elements present in semitectate and intectate pollen (i.e., the reticulum, the rod-like columellae, etc.) are here defined as comprising *simultaneously* both structure and sculpturing since sculpturing in semitectate and intectate pollen (at least within primitive angiosperms of the subclass Magnoliidae) appears to be homologous with exine structure that previously existed as part of pollen grains which were tectate. In semitectate and intectate pollen the scanning electron microscope may show both structure and sculpturing simply because of this definition. It should also be pointed out that one may observe structure using the scanning electron microscope even in tectate pollen grains if the grains have been broken (cf. Fig. 7D). Finally, it must be mentioned that some magnoliid angiosperms have pollen grains with a morphologically homogeneous exine which appears to be primitively devoid of columellae. Such pollen has been designated "atectate." With reference to sculpturing, tectate pollen may be described as supra-ornate because the sculpturing elements are upon the tectum, while semitectate and intectate pollen may be designated per-ornate because they lack a tectum and their surface ornamentation represents simultaneously structure and sculpturing.

Exine Sculpturing.—Exine sculpturing consists of any exposed surface details of the pollen wall. The same sculpturing terms are used in the case of tectate and intectate pollen, with the understanding that the sculpturing in tectate grains is supratectal and distinct from the underlying structure, while sculpturing and structure are synonymous in intectate grains. Semitectate grains by definition are sculptured and are usually reticulate, the reticulum constituting both structure and sculpturing. Major exine sculpturing types (Figs. 8–9) include the following: (1) psilate (smooth); (2) foveolate (pitted); (3) fossulate (grooved); (4) scabrate (with very fine projections, usually defined as less than 1μ); (5) verrucate (warty); (6) baculate (with rod-like sculpturing elements); (7) pilate (with pila, i.e., rod-like sculpturing elements with swollen heads; synonym: clavate[7]; (8) gemmate (with sessile pila); (9) echinate (spiny); (10) rugulate (with elongate sculpturing elements irregularly distributed tangentially over the pollen surface); (11) striate (with elongate, more or less parallel sculpturing elements distributed tangentially over the pollen surface); and (12) reticulate (with sculpturing elements forming an open network or reticulum over the pollen surface). Should the sculpturing elements be supra-tectal (i.e., the pollen is supra-ornate), the prefix supra- may be used before the sculpturing type, e.g., supra-verrucate, supra-baculate, supra-echinate, etc. Sculpturing in per-ornate pollen lacking a tectum may be designated by use of the prefix per- before the sculpturing type, e.g., per-verrucate, per-baculate, per-echinate, etc.

Evolution of Pollen Wall Architecture.—Evolutionary trends in pollen wall architecture offer great potential as sources of phylogenetic information of major importance. However, to date most studies have not attempted to examine wall architecture with specific evolutionary goals in mind, but have rather concentrated on descriptive or developmental aspects of a number of usually unrelated taxa.

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[7] Should the pila be arranged in a reticulate pattern but not actually united into a true reticulum, the grains may be described as retipilate.

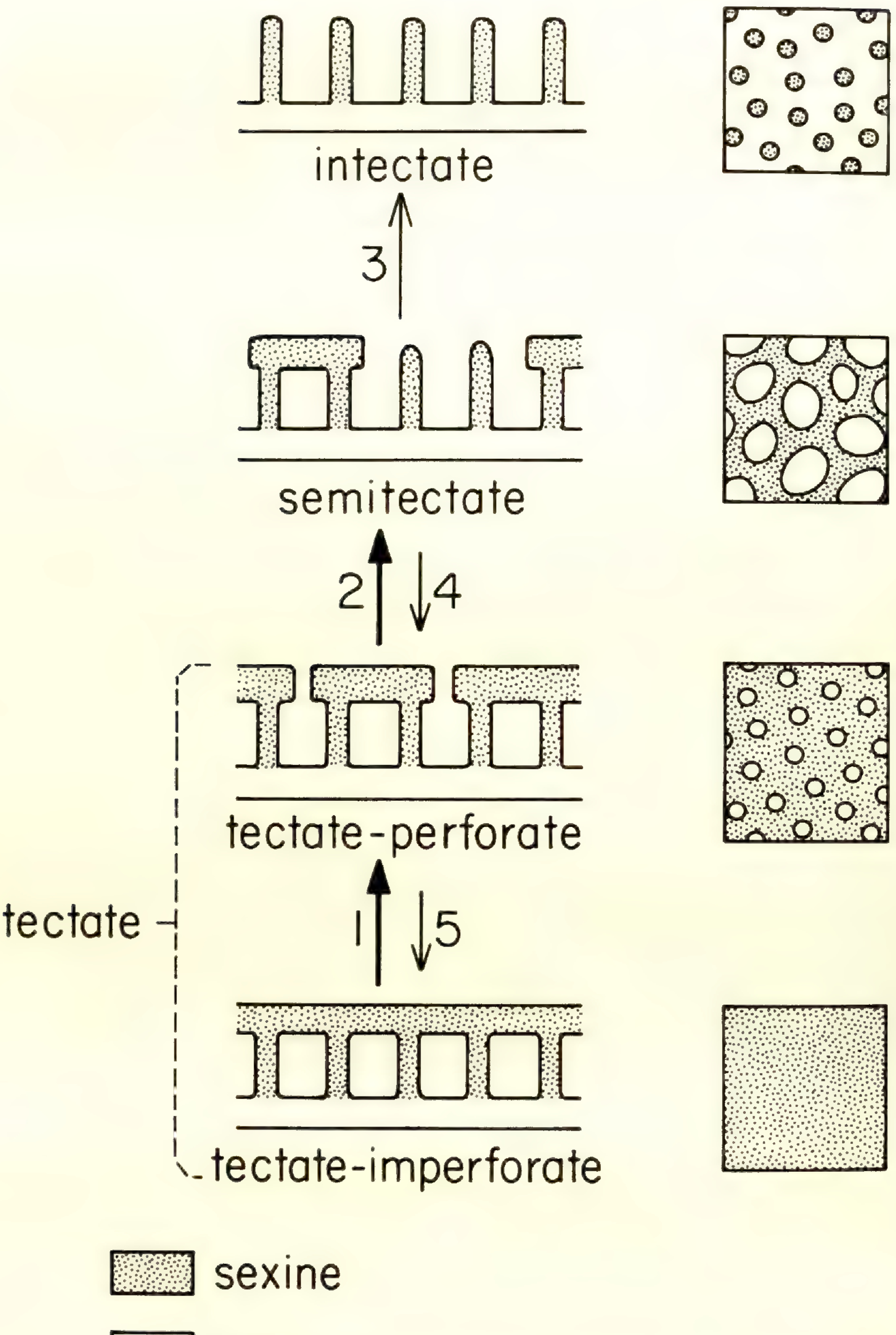

FIGURE 10. Evolutionary trends in angiosperm exine structure types. Cross-sectional views to the left, surface views to the right. Strong arrows 1 and 2 indicate more common stages; weaker arrow 3 indicates less frequently observed stage. Arrows 4 and 5 indicate possible reversibility of the trend, particularly in its earlier stages. The most primitive atectate type of exine structure is not shown.

More comparative studies on the nature of the pollen wall in related groups of plants are required to realize the full phylogenetic potential of pollen wall morphology. Studies presently available, however, appear to reveal the following general evolutionary trends. The pollen wall in most angiosperms consists of both intine and exine. Reduced pollen with little or no exine, as often observed in aquatic angiosperms, clearly represents an advanced condition. Studies in progress on ranalean pollen suggest that a great amount of phylogenetic information resides in the stratification of the exine itself. Preliminary investigations (Walker & Kemp, 1972) have shown that the ratio of nexine to sexine is phylogenetically important. Current studies indicate that presence or absence of endexine and foot-layers, as well as their thickness relative to other layers of the pollen wall, are also phylogenetically useful characters. However, current data are insufficient to allow generalizations of major evolutionary trends in exine stratification at this time. Study of primitive angiosperm families of the subclass Magnoliidae has revealed that some extant angiosperms possess atectate pollen, primitively devoid of columellae (Walker, 1974a; Walker & Skvarla, 1975). From such pollen, a major evolutionary trend in angiosperm exine structure appears to run from pollen which is tectate-imperforate to tectate-perforate and semitectate pollen, and thence more rarely to intectate pollen (Fig. 10; Walker, 1974b). Thus, it appears that sculpturing in angiosperm pollen was primitively supra-ornate, later per-ornate. With reference to exine sculpturing types, primitive angiosperm pollen appears to have been more or less psilate (Walker, 1975), although sculpturing itself undoubtedly represents a more or less reversible character which must be interpreted in terms of individual correlations observed within any given taxa. For more detailed discussions, see Walker (1976).

POLLEN-UNIT

The pollen-unit (Walker, 1971b) is the grouping in which pollen is found at maturity within the anther locules of the stamen. Most pollen at maturity consists of solitary grains or monads (Fig. 11A). However, some or all members of approximately 55 families of angiosperms (representing 43 dicot and 12 monocot families) have mature pollen grains in pollen-units other than monads, i.e., in dyads, tetrads, pseudomonads (cryptotetrads), polyads, massulae, or pollinia (Table 2).

Dyads.—The regular production of dyads which consist of two pollen grains held together as a unit is rather infrequent, and occurs chiefly in the two families Podostemaceae and Scheuchzeriaceae.

Tetrads (Including Pseudomonads or Cryptotetrads).—The most common pollen-unit other than monads is the tetrad, which represents a retention of the four products resulting from meiosis of the pollen mother cell. However, in connection with some pollen characters, e.g., particularly pollen grain shape, a clear distinction must be made between the cytological-embryological meiotic tetrad and the mature pollen tetrad of the palynologist. Tetrads may be classified into tetrad types (Fig. 12) according to the spatial arrangement of the individual pollen grains within the tetrad. In this regard, there are two fundamentally different types of pollen tetrads—uniplanar with all grains (and particularly their

TABLE 2. Angiosperm families with pollen-units other than monads.[a]

DICOTYLEDONS

Magnoliidae
+++Lactoridaceae
+++Winteraceae
++Annonaceae (also polyads)
Monimiaceae
Nymphaeaceae

Ranunculidae
Berberidaceae
Papaveraceae

Caryophyllidae
Didiereaceae (possibly tetrads)

Hamamelididae
+++Myrothamnaceae
Eucommiaceae

Dilleniidae
+++Sarcolaenaceae
Actinidiaceae
Guttiferae
Tiliaceae
Lecythidaceae
+++Nepenthaceae
+++Droseraceae
Begoniaceae
Datiscaceae
Cucurbitaceae

+++Ericaceae
++Epacridaceae
+++Empetraceae
+++Pyrolaceae

Rosidae
Saxifragaceae
Rosaceae
++Leguminosae (also polyads)
++Podostemaceae (dyads, possibly polyads)
+Onagraceae
Cornaceae
Rafflesiaceae
+Hippocrateaceae (also polyads)
Celastraceae (also polyads)
Sapindaceae

Asteridae
++Gentianaceae (also polyads)
++Apocynaceae
+++Asclepiadaceae (also polyads, massulae, and pollinia)
Solanaceae
+Bignoniaceae
Pedaliaceae
+++Hydrostachyaceae
Goodeniaceae
+Rubiaceae

MONOCOTYLEDONS

Alismatidae
Hydrocharitaceae
+++Scheuchzeriaceae (dyads)

Arecidae
Araceae

Liliidae
Philydraceae
Liliaceae (~ Amaryllidaceae)
++Velloziaceae

+++Orchidaceae (also polyads, massulae, and pollinia)

Commelinidae
+++Juncaceae
+++Thurniaceae
+++Cyperaceae (pseudomonads or cryptotetrads)
+++Typhaceae
Bromeliaceae

[a] Based mostly on data of Erdtman (1945b, 1966); tetrads present unless otherwise stated. The symbols in front of families indicate that tetrads or other pollen-units larger than monads occur respectively in all members or the overwhelming majority of the family (+++), in a significant number of genera in the family (++), or in several genera in the family (+). No symbols before a family indicates that pollen-units other than monads are very rare in the family or may only be found in certain individual plants of a species (e.g., pollen tetrads found in material from one particular tree of *Eucommia*).

polar axes) in the same plane and multiplanar with grains (and their polar axes) in more than one plane. Uniplanar tetrads may be tetragonal (square, isobilateral; Fig. 11C), rhomboidal (Fig. 11D), linear, or T-shaped, while multiplanar tetrads may be tetrahedral (Fig. 11E) or decussate (cross-shaped; Fig. 11F). As a rule, the monosulcate pollen of magnoliid dicots and monocots occurs in tetragonal tetrads, while the tricolpate pollen of the non-magnoliid dicotyledons is generally found in tetrahedral tetrads.

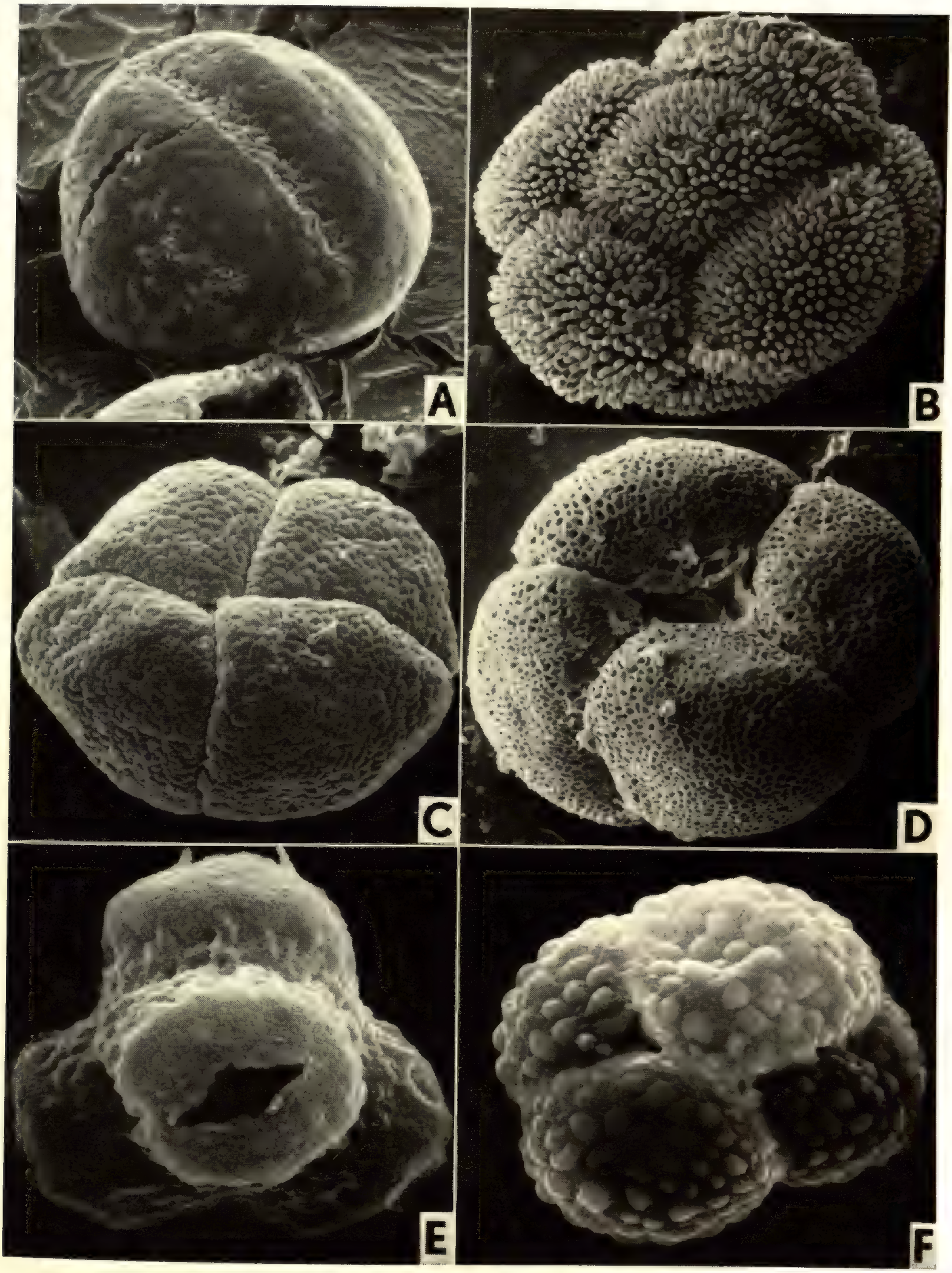

FIGURE 11. Types of pollen-units.—A. Monad; × ca. 1840 (*Warburgia ugandensis* Sprague; Canellaceae).—B. Polyad (octad); × ca. 700 (*Trigynaea caudata* (R. E. Fries) R. E. Fries; Annonaceae).—C. Tetragonal tetrad; × ca. 970 (*Uvariastrum hexaloboides* (R. E. Fries) R. E. Fries; Annonaceae).—D. Rhomboidal tetrad; × ca. 375 (*Annona muricata* L.; Annonaceae).—E. Tetrahedral tetrad; × ca. 1500 (*Lactoris fernandeziana* Phil.; Lactoridaceae).—F. Decussate tetrad; × ca. 1050 (*Orophea luzonensis* Merr. = *Pseuduvaria* sp.; Annonaceae).

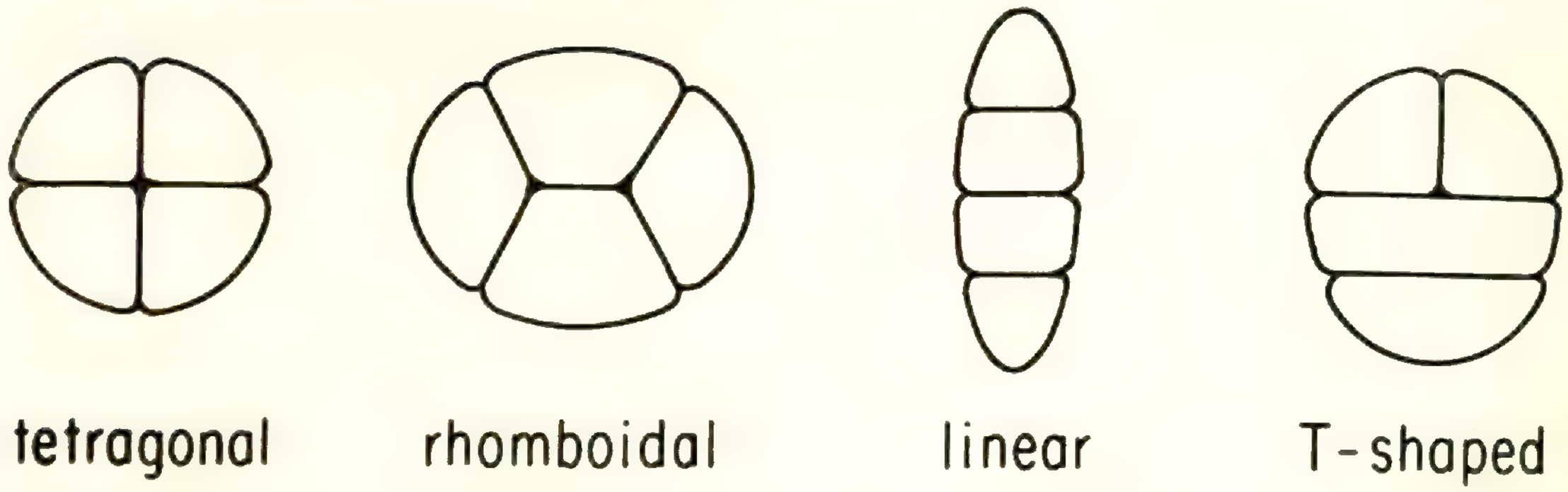

FIGURE 12. Pollen tetrad types. See text for discussion.

Of the approximately 50 angiosperm families with pollen in tetrads (Table 2), 13 have their pollen grains entirely or almost entirely in tetrads, six have a significant number of genera with some or all species with tetrads, four have several genera with pollen in tetrads, and the remainder (27 families) have tetrads only rarely. The Cyperaceae have pseudomonads (cryptotetrads) which are morphological monads that are actually homologous to tetrads since in this family the wall of the apparent solitary pollen grain is actually formed by the pollen mother cell that contains a pollen tetrad in which three of the four grains fail to develop.

Polyads.—Polyads (Fig. 11B), which are pollen-units of a definite number greater than four, e.g., octads, 16's, etc.,[8] are much less common than tetrads and have been reported only in the following seven angiosperm families: Annonaceae, Leguminosae (Mimosoideae), Hippocrateaceae, Celastraceae, Gentianaceae,

[8] At least two polyads or massulae must occur in each anther locule, otherwise by definition a pollinium, not a polyad or massula, is present.

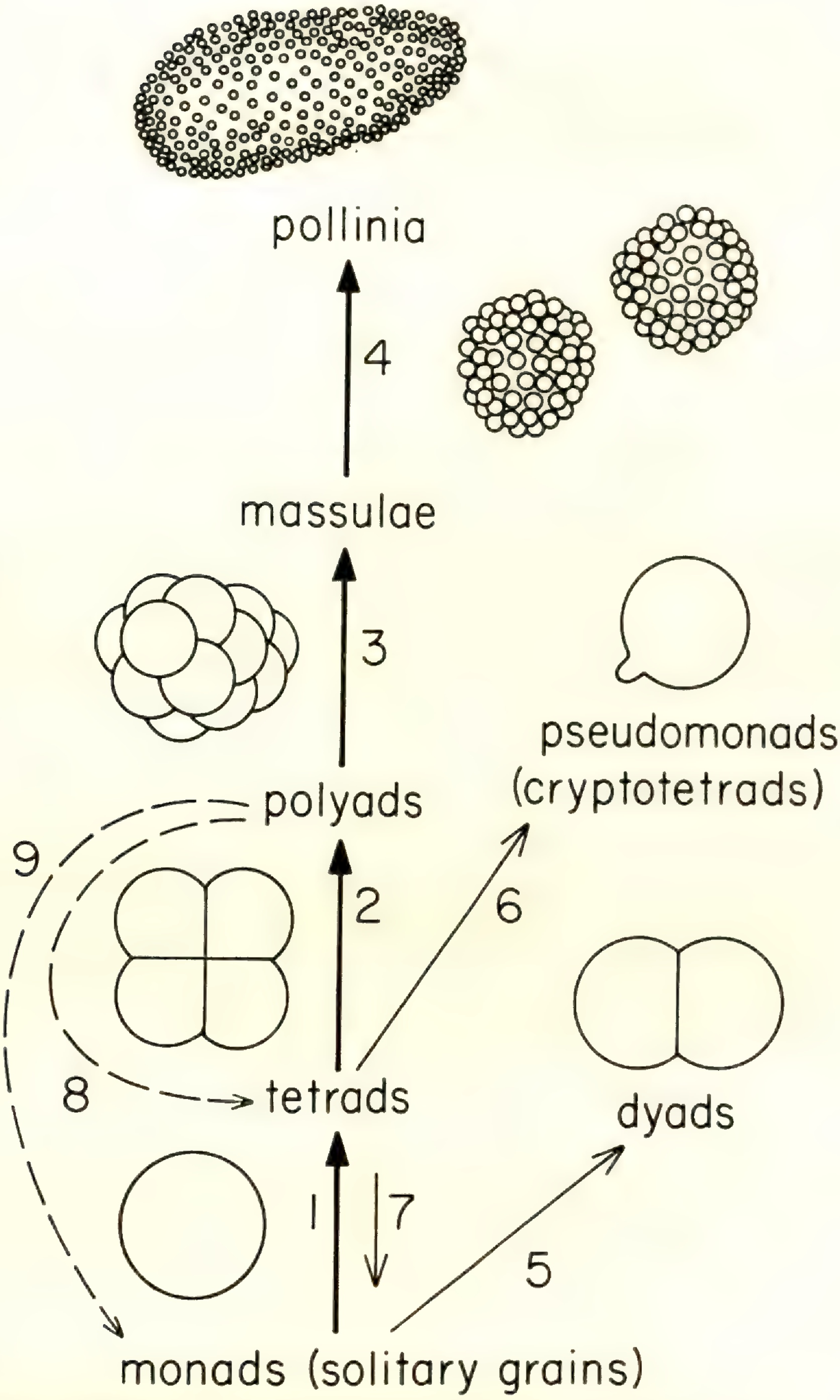

FIGURE 13. Evolutionary trends in angiosperm pollen-units. See text for discussion.

Asclepiadaceae, and Orchidaceae. Polyads may consist of connate but individually discernible tetrads, or they may be more or less irregular with no individual tetrads visible.

Massulae.—Massulae are pollen-units that are usually larger than polyads in which the number of individual pollen grains is not ascertainable due to a large

number of grains and/or a large amount of pollen fusion.[8] The Asclepiadaceae and Orchidaceae are the only two families with massulae.

Pollinia.—A pollinium consists of the entire pollen-mass of one or more anther locules fused together as a unit. Pollinia, like massulae, are restricted to the families Asclepiadaceae and Orchidaceae.

Evolution of Pollen-Units.—Monads clearly represent the basic angiosperm pollen-unit. Regularly occurring, permanent dyads have independently evolved from monads in two families (one dicotyledonous and the other monocotyledonous). Regularly produced permanent tetrads have evolved separately in a number of lines, and represent an advanced character over solitary grains. In some instances, however, monads may have secondarily evolved from tetrads (Walker, 1971b), and in such cases solitary grains represent an advanced rather than a primitive character-state. Pseudomonads (cryptotetrads) apparently have evolved from permanent tetrads since the only family that has pseudomonads (the Cyperaceae) appears to be related to the more primitive family Juncaceae which has permanent tetrads. Polyads occur much less frequently than tetrads but have also evolved independently a number of times. Since in every family that has polyads, some taxa (often clearly the more primitive) possess tetrads, it seems evident that polyads have arisen from tetrads. Also, as previously mentioned, some polyads consist of individually discernible tetrads. Normally polyads represent a more advanced grade than tetrads, but it should not be overlooked that in some lines polyads may have given rise secondarily to tetrads or even to monads. Massulae and pollinia represent the most advanced pollen-units and occur only in two families of angiosperms. Interestingly, both of these families (Asclepiadaceae and Orchidaceae) have tetrads and polyads in their more primitive members. Figure 13 outlines evolutionary trends in angiosperm pollen-units.

POLLEN GRAIN POLARITY

Polarity is a quality inherent in a body that has opposite parts or poles, and which as a consequence has one main axis of symmetry. Pollen grain polarity is undoubtedly due to the fact that all pollen results from meiosis of pollen mother cells and thus all pollen grains are at one time or another united together as members of a meiotic pollen tetrad. Individual pollen grains may thus be likened to a globe with poles and an equator (cf. section above, POLLEN APERTURES). The polar axis of a pollen grain, which may also be termed the main or vertical axis, is generally also an axis of symmetry, and in globe-shaped (as opposed to boat-shaped) pollen grains usually an axis of rotation as well. The equatorial plane of a pollen grain perpendicularly bisects the polar axis. The part of the equatorial plane enclosed by the equator of the pollen grain may be called the equatorial outline. The equatorial plane contains two or more horizontal symmetry axes which are known as the equatorial axes. Horizontal symmetry axes (equatorial axes) are the lines which represent the intersection of any vertical planes of symmetry that a particular pollen grain may have with the equatorial plane, such vertical planes of symmetry going through the vertical symmetry axis or polar axis of the pollen grain (cf. section below, POLLEN GRAIN SYMMETRY). For example, monosulcate pollen grains have two equatorial axes which are mutually perpen-

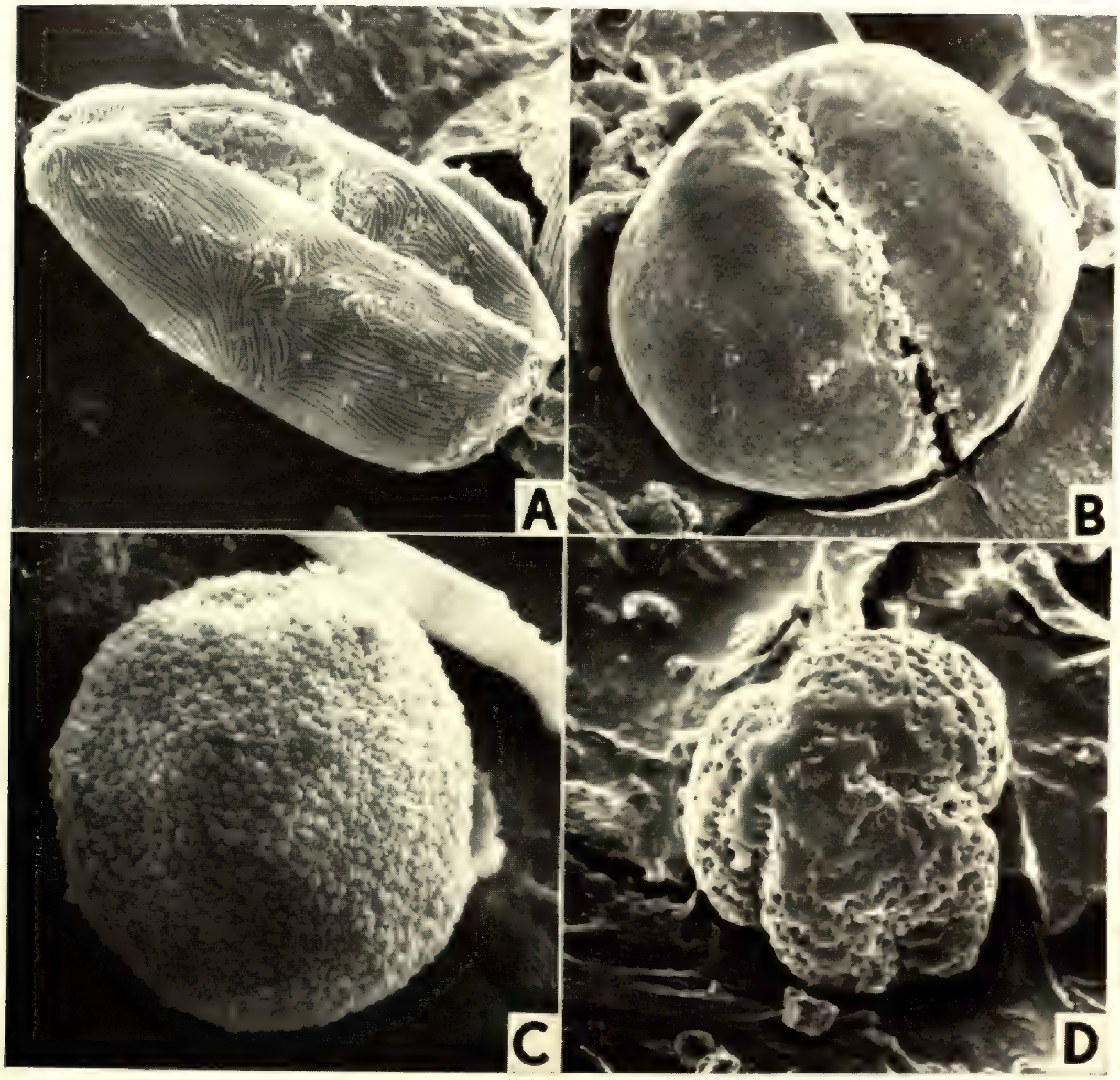

FIGURE 14. Types of pollen grain polarity and symmetry.—A. Heteropolar, bilateral (monosulcate) pollen (*Cabomba caroliniana* Gray; Cabombaceae). Equatorial view; × ca. 1370.—B. Heteropolar, isobilateral (monosulcate) pollen (*Dialyanthera otoba* (Humb. & Bonpl.) Warb.; Myristicaceae). Presumed distal-polar view; × ca. 1500.—C. Apolar, radiosymmetric (inaperturate) pollen (*Xymalos monospora* (Harv.) Baill.; Monimiaceae); × ca. 2810.—D. Isopolar, radiosymmetric (tricolpate) pollen (*Lardizabala biternata* Ruiz & Pav.; Lardizabalaceae). Polar view; × ca. 1460.

dicular, inaperturate pollen has an infinite number of equatorial axes, dicolpate, diporate, and disulculate pollen grains have two mutually perpendicular equatorial axes, and tricolpate and triporate pollen has three equatorial axes, none of which is perpendicular to each other. It must be emphasized that there is a fundamental difference between the polar axis and an equatorial axis in that there is only one polar axis (vertical symmetry axis) while there are always at least two, sometimes (in the case of inaperturate pollen) even an infinite number of equatorial axes (horizontal symmetry axes).

Pollen grains may be without distinct polarity and apolar (Fig. 14C), i.e., without discernible poles once the grains have separated from the meiotic pollen tetrad, or pollen may be polar with recognizable poles even after the grains have

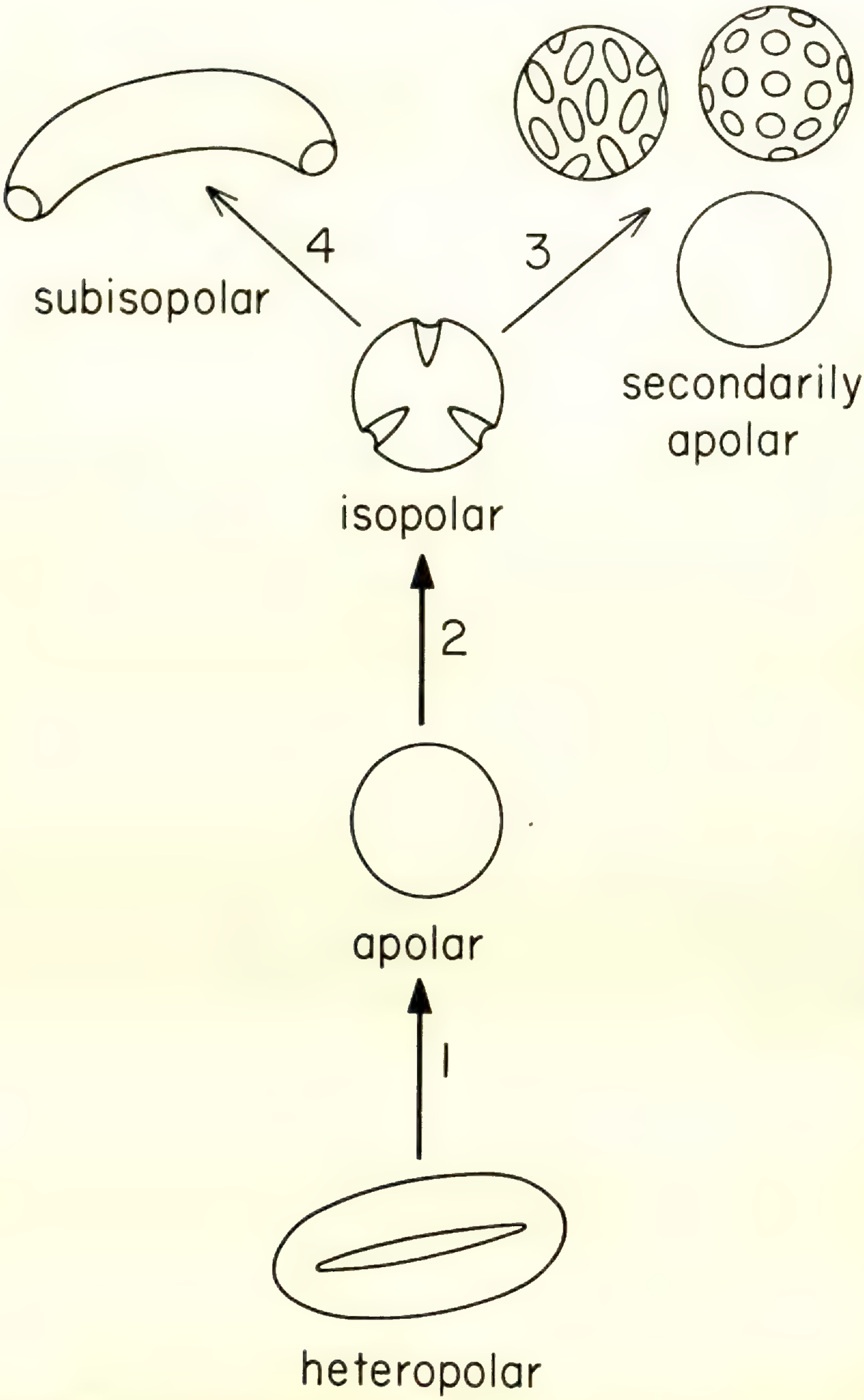

FIGURE 15. Major evolutionary trends in the polarity of angiosperm pollen. Heteropolar and isopolar pollen shown in polar view; subisopolar pollen shown in more or less equatorial view. See text for discussion.

separated from the pollen tetrad. Pollen that at first appearance seems to be apolar, but which upon closer examination proves to possess a more or less distinct polarity may be designated cryptopolar. Polar pollen grains may be further characterized as isopolar (Fig. 14D), with the equatorial plane dividing the grain into similar halves, or heteropolar (Figs. 14A, B), with the polar faces markedly dissimilar. Grains which usually have a more or less curved equatorial plane and possess only slight differences between the distal and proximal faces (e.g., one face may be very convex, the other less convex, plane, or even concave) may be termed subisopolar.

Pollen grain polarity is of two types—apparent and absolute. Apparent polarity is usually due to the aperture(s) present and/or to possession of a distinct vertical axis of symmetry, which usually appears as an axis of rotation also. Less frequently, apparent polarity may be related to exine sculpturing, either alone or in conjunction with apertures and/or a vertical axis of symmetry-rotation. Apparent pollen grain polarity is usually the same as absolute polarity, but it is essential for clear palynological thinking to keep the distinction between apparent and absolute pollen grain polarity in mind. The former is based on indirect but normally reliable clues observed in solitary pollen grains (apertures, sculpturing, a vertical axis of symmetry-rotation), while the latter is based on direct observation of pollen tetrads. In the majority of cases absolute pollen polarity must be inferred from apparent pollen polarity since most pollen is shed in the form of monads.

Evolution of Pollen Grain Polarity.—Major evolutionary trends in the polarity of angiosperm pollen are outlined in Fig. 15. Since polarity is largely determined by aperture condition, the primitive type of angiosperm pollen grain polarity (heteropolarity) is directly related to possession of a monosulcate pollen aperture. From such heteropolar pollen the main evolutionary trend has been to apolar inaperturate grains, and from pollen of this type to the basic isopolar colpate pollen of non-magnoliid dicotyledons.[9] Apolar inaperturate, rugate, and forate pollen has been derived secondarily from isopolar colpate pollen within some non-magnoliid dicotyledons. In other non-magnoliid dicots, isopolar pollen grains have given rise to subisopolar pollen. Evolutionary trends in spore as well as pollen grain polarity have been discussed by Chaloner (1970).

POLLEN GRAIN SYMMETRY

Symmetry is the quality inherent in a body which is capable of division into similar or equal halves (i.e., mirror images). Pollen grain symmetry is the correspondence on opposite sides of a median plane in the size and shape of the resulting halves, and similarly in the number, relative position, and type of pollen apertures present. Such median planes are known as symmetry planes. In addition, pollen grains may have symmetry axes. Symmetry axes are lines which run through the center of the pollen grain and either go through both poles (the vertical symmetry axis or polar axis) or lie in the equatorial plane and represent the intersection of all vertical planes of symmetry with the equatorial plane

[9] A minor trend from heteropolar, anasulcate pollen directly to isopolar, zonizonasulculate pollen via an anazonasulculate intermediary without an apolar, inaperturate intermediate stage may be observed within the pollen of the family Nymphaeaceae.

TABLE 3. Number of symmetry axes and planes in different types of pollen grains.

Pollen Type	Vertical Axes (polar axis)	Vertical Planes (polar planes)	Horizontal Axes (equatorial axes)	Horizontal Planes (equatorial plane)
Heteropolar, monosulcate pollen	1	2	2	0
Apolar, inaperturate pollen	1	∞	∞	1
Isopolar pollen with 2–many, equidistant, equatorial apertures	1	Same number as equatorial apertures, i.e., 2–many	Same number as equatorial apertures, i.e., 2–many	1
Total Range	1	2–∞	2–∞	0–1

of the pollen grain (horizontal symmetry axes or equatorial axes), such vertical planes of symmetry going through the vertical symmetry axis (polar axis) of the pollen grain. Thus, symmetry axes and planes may be either vertical or horizontal, depending on whether they go through the poles or the equator of the pollen grain. Pollen grains have only one vertical *axis* of symmetry (the polar or main axis), while there may be from two to an infinite number of vertical *planes* of symmetry (i.e., polar symmetry planes). On the other hand, there may be one or no horizontal planes of symmetry (i.e., equatorial symmetry planes), while there are always at least two and sometimes an infinite number of horizontal axes of symmetry (i.e., equatorial axes). In any given pollen grain the number of equatorial axes always equals the number of vertical planes of symmetry. Horizontal symmetry axes and vertical symmetry planes always go through the polar axis. Horizontal symmetry axes perpendicularly bisect the polar axis, and like vertical symmetry planes they may be mutually perpendicular. By definition, pollen grain symmetry is based on the planes of symmetry that exist in a particular grain *as seen from polar view*, i.e., on vertical, not horizontal, symmetry planes.[10] With reference to three common types of pollen grains, the number of vertical symmetry planes are as follows: two in heteropolar, monosulcate grains; infinite in apolar, inaperturate grains; and the same as the number of apertures in isopolar grains with equatorial apertures that are equidistant. On the other hand, all heteropolar pollen grains would have no horizontal symmetry planes, while both apolar inaperturate grains and isopolar grains with two or more equidistant equatorial apertures would have one horizontal symmetry plane (cf. Table 3).

Pollen grain symmetry is largely determined by grain shape and apertures.

[10] For the purpose of symmetry determination heteropolar grains must be observed from the pole which possesses the aperture(s). If both poles should possess apertures and they are dissimilar in shape, number, or position from one pole to the other, then the grain could have two different types of symmetry depending on the pole observed. In such cases the two symmetry types should be recorded with respect to occurrence on either the distal or proximal pole, if possible.

Symmetry as applied to pollen grains is based on (1) the number of vertical planes of symmetry that exist in a particular grain, (2) whether the equatorial axes of the grain are all of equal length or not, i.e., generally whether the equatorial outline is circular or not, and (3) the nature of the aperture(s) present. Rarely, pollen may be more or less asymmetric due to irregular grain shape resulting from occurrence of random protuberances of the exine, i.e., protuberances of the outer pollen wall itself, not merely localized variation in surface sculpturing elements, or because of the unsymmetrical distribution of apertures preventing a division into similar halves. Symmetric pollen grains, which are capable of division into similar halves, may be further classified as radiosymmetric or bisymmetric. Radiosymmetric pollen (Figs. 14C, D) is divisible into equal symmetrical portions by any of three or more (up to infinity) equilong vertical planes of symmetry passing through the polar axis, i.e., all three or more equatorial axes are equilong. Bisymmetric grains are doubly symmetrical, i.e., divisible into two similar halves by either of two (never three or more) mutually perpendicular vertical planes of symmetry passing through the polar axis. Bisymmetric pollen may be either bilateral or isobisymmetric. Bilateral[11] pollen grains (Fig. 14A) have two mutually perpendicular vertical planes of symmetry passing through the polar axis which are of different length, i.e., the two equatorial axes are not equilong and the equatorial outline of the grain is elliptical, oval, etc., but not circular. Isobisymmetric grains[12] have two mutually perpendicular vertical planes of symmetry passing through the polar axis which are the same length, i.e., the two equatorial axes are equilong and the equatorial outline of the grain is usually more or less circular. Isobisymmetric pollen may be either isobilateral or biradial. Isobilateral pollen grains (Fig. 14B) are isobisymmetric grains that are heteropolar and monosulcate, their isobisymmetry being a function largely of the elongate nature of their polar aperture. They are essentially bilateral pollen grains with a round rather than elongate equatorial outline. Biradial pollen is also isobisymmetric, but biradial grains are isopolar and equatorially di-aperturate (i.e., either disulculate-diulculate or dicolpate-diporate), their isobisymmetry being chiefly a function of their aperture number (two). They are essentially radial pollen with two rather than three or more apertures.

Evolution of Pollen Grain Symmetry.—Major evolutionary trends relating to pollen grain symmetry in angiosperms are outlined in Fig. 16. Primitive boat-shaped, monosulcate pollen has bilateral symmetry. From this primitive type of symmetry the common radiosymmetry of the majority of dicotyledonous pollen

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[11] Pollen which is boat-shaped, heteropolar, and monosulcate (or elongate, isopolar, and equatorially di-aperturate, e.g., dicolpate, diporate, disulculate, etc.) has been incorrectly described almost universally by palynologists as bilateral. Bilaterally symmetrical objects are divisible by only a single plane (i.e., are monosymmetric), not two, as are boat-shaped, bisymmetric, monosulcate pollen grains; pollen of this type is more correctly described as anisobisymmetric. However, the more familiar term bilateral, as defined above, has been retained for use in palynological descriptions with the understanding that mathematically this usage of the term bilateral is incorrect, anisobisymmetric being the more proper term.

[12] Erdtman (1966) improperly considered pollen grains with this type of symmetry as radiosymmetric. Since radiosymmetric objects by definition must have three or more planes of symmetry, pollen of this type has been designated as isobisymmetric.

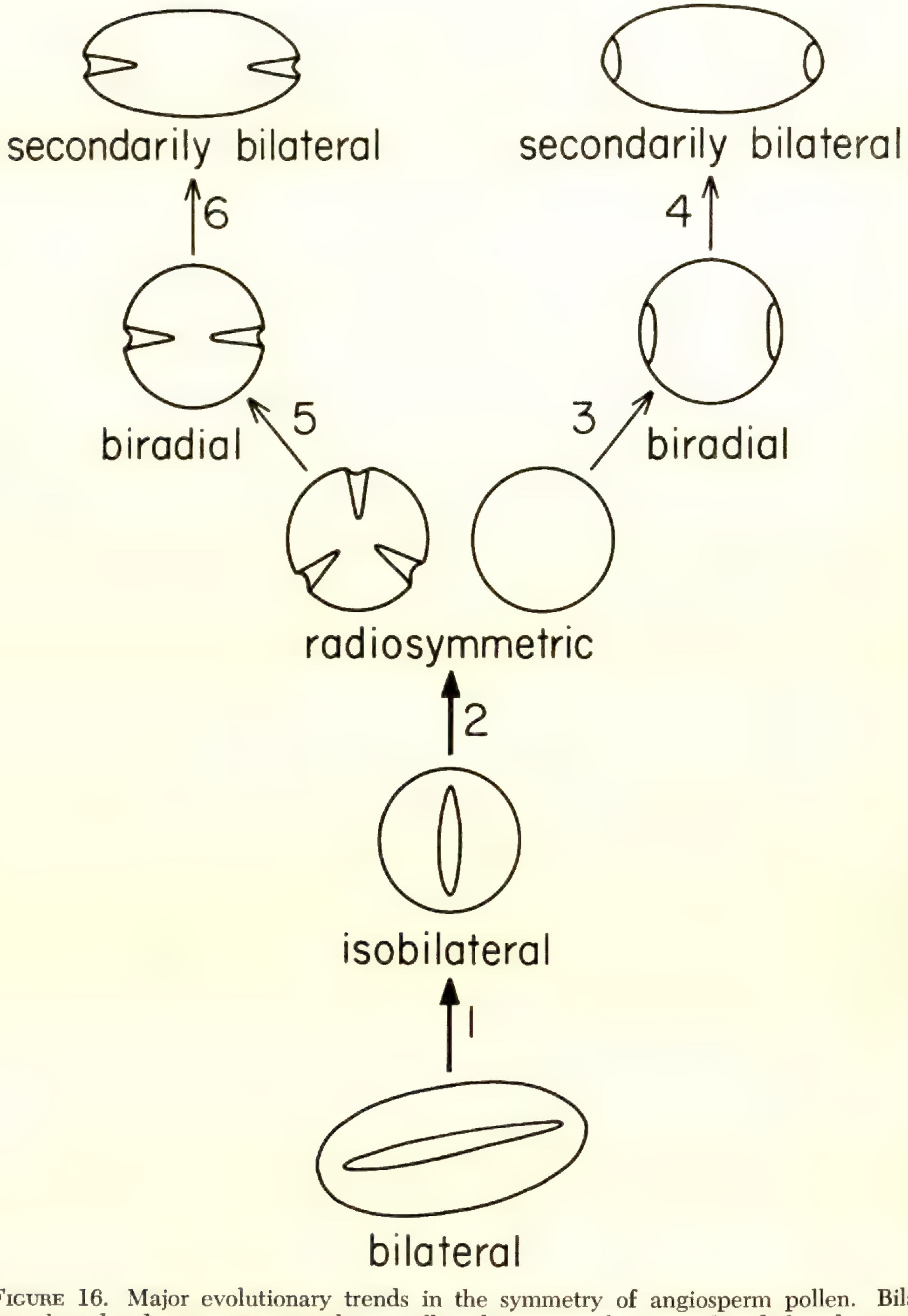

FIGURE 16. Major evolutionary trends in the symmetry of angiosperm pollen. Bilateral, isobilateral, and radiosymmetric tricolpate pollen shown in polar view; biradial and secondarily bilateral pollen all shown in equatorial view. See text for discussion.

has evolved, apparently via an isobilateral intermediate stage which retains a sulcus combined with a circular equatorial outline. Biradial pollen (e.g., dicolpate, diporate, disulculate pollen, etc.) has evolved in a number of families from radially symmetrical grains because of the occurrence of only two apertures. Such biradial pollen may change its shape from spherical to equatorially elongate, thus producing pollen which is secondarily bilateral.

POLLEN GRAIN SHAPE

Shape is the spatial form of a body. Pollen grain shape is correlated largely with aperture type which in turn is more or less correlated with polarity and symmetry. It should be pointed out that method and length of pollen preparation may cause the shape of pollen grains to vary considerably. With reference to shape, angiosperm pollen may be either nonfixiform (without definite shape) or fixiform (with definite shape). The rare nonfixiform type of pollen occurs in many marine angiosperms such as *Zostera*, in which the pollen, that may be over 2000μ long, is threadlike. Normal, fixiform angiosperm pollen may be divided into two basic shape classes—boat-shaped and globose (globe-shaped). Boat-shaped pollen (Figs. 17A–C), as the name implies, is boat-like with a short polar axis and one equatorial axis that is longer than the other. Its most prominent axis of rotation coincides with the longer equatorial axis and its polar axis is generally not a prominent axis of rotation. Its equatorial outline is usually more or less elliptical to oblong, and its polarity is due to apertures present, not its symmetry. Boat-shaped pollen may be further divided into a number of subtypes depending on the ratio of the longer equatorial axis to the shorter. If this ratio is greater than 1.00 but less than 1.50, the pollen is boat-shaped-elliptic (Fig. 17C), while pollen with a ratio between 1.50 and 1.99 is boat-shaped-oblong (Fig. 17B). Any pollen grains with a ratio equal to or greater than 2.00 are described as boat-shaped-elongate (Fig. 17A).

Globose pollen (Figs. 17D–F), on the other hand, is basically globe-shaped with its equatorial axes all the same length and its polar axis is generally a prominent axis of rotation. Its equatorial outline is usually more or less circular or some modification thereof such as triangular, lobed, etc., and its polarity generally results from both its symmetry and its apertures. The shape of most globose pollen is that of an ellipsoid with the polar axis as axis of rotation. Globose pollen may also be further subdivided, depending on the ratio of polar to equatorial axes. If both polar and equatorial axes are the same length, the pollen is spherical (Fig. 17D). If the polar axis is shorter than the equatorial axes, i.e., the grains are compressed along the polar axis, the pollen is flattened or oblate (Fig. 17E).[13] And finally, if the polar axis is longer than the equatorial axes, i.e., the grains are compressed around the equator rather than along the polar axis, the pollen is prolate (Fig. 17F).[13] A more comprehensive classification of globose pollen is outlined in Table 4, which is slightly modified from Erdtman (1966). At times, di-aperturate, globose pollen, e.g., disulculate or diporate pollen, may have a more or less elliptical to oblong equatorial outline, with one equatorial axis longer than the other. Globose pollen of this type (which is also secondarily bilateral) is described as globose-elliptic, -oblong, or -elongate, depending on whether the ratio of the longer equatorial axis to the shorter is greater than 1.00 but less than 1.50, is between 1.50 and 1.99, or is equal to or greater than 2.00.

The outline of a pollen grain as seen in polar view with the polar axis directed towards the observer is known as the pollen amb. In most pollen the amb coincides

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[13] The terms oblate and prolate are used here in a broader sense than that of Erdtman (1966). It is suggested that Erdtman's oblate and prolate be replaced by the terms *euoblate* and *euprolate*, so that the former may be used as broader grouping terms.

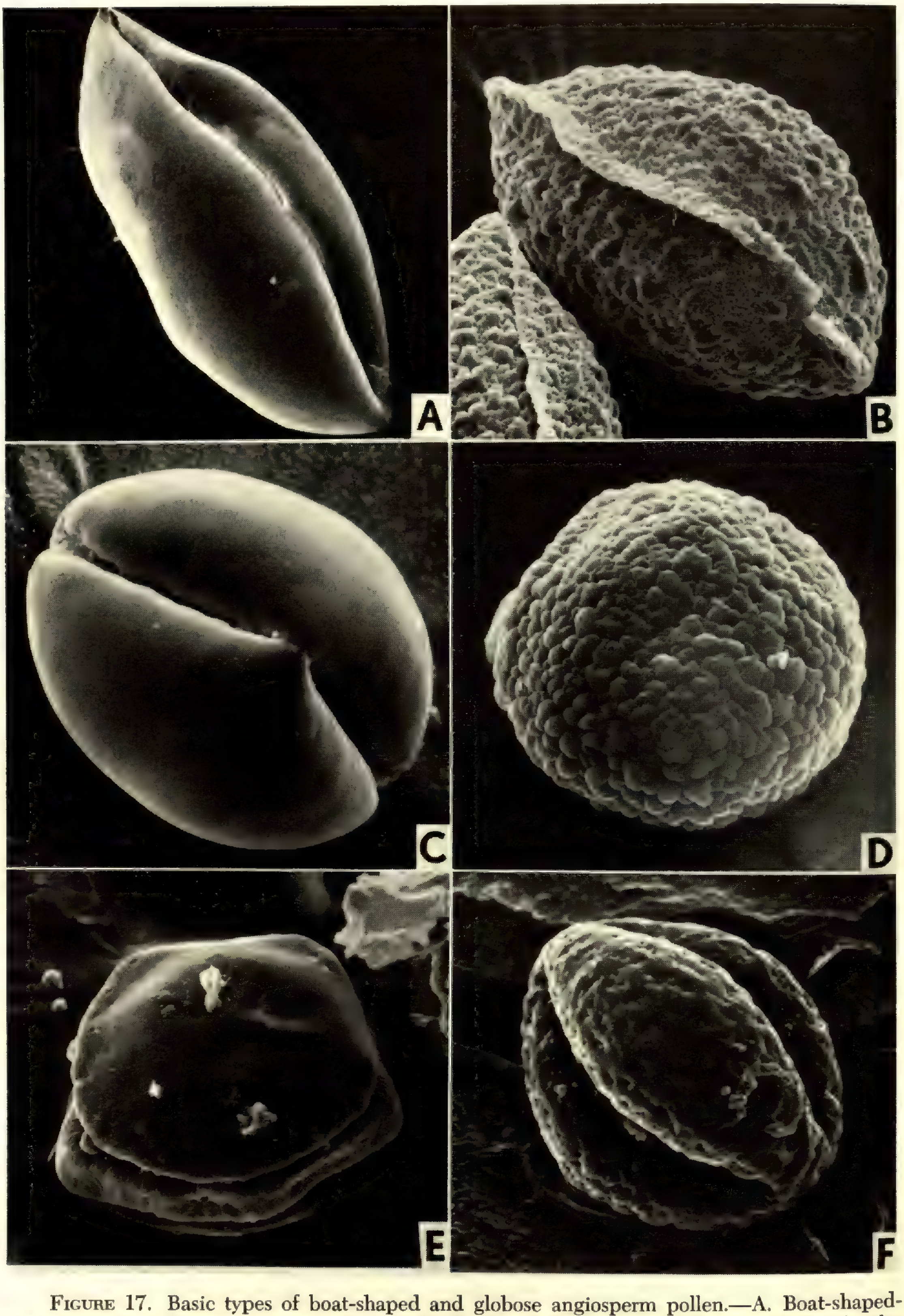

Figure 17. Basic types of boat-shaped and globose angiosperm pollen.—A. Boat-shaped-elongate pollen (*Anaxagorea costaricensis* R. E. Fries; Annonaceae). Presumed distal-polar view; × ca. 1380.—B. Boat-shaped-oblong pollen (*Liriodendron tulipifera* L.; Magnoliaceae). Presumed distal-polar view; × ca. 1440.—C. Boat-shaped-elliptic pollen (*Degeneria vitiensis* I. W. Bailey & A. C. Smith; Degeneriaceae). Distal-polar view; × ca. 2630.—D. Globose-

TABLE 4. Classification of globose pollen based on ratio of polar to equatorial axes (P/E).

Designation	P/E ratio
Prolate	
Perprolate	≧ 2.00
Euprolate	1.34–1.99
Subprolate[a]	1.15–1.33
Prolate spheroidal[a]	1.01–1.14
Spherical	1.00
Oblate	
Oblate spheroidal[a]	0.88–0.99
Suboblate[a]	0.76–0.87
Euoblate	0.51–0.75
Peroblate	≦ 0.50

[a] Subprolate, prolate spheroidal, oblate spheroidal, and suboblate pollen grains may be grouped together under the category of subspheroidal pollen.

with the equatorial outline of the grain, but this is not the case in equatorially constricted pollen. The amb in tricolpate (and tricolpate-derived) globose pollen especially may be of some phylogenetic significance, and there are a number of possible amb types in such pollen (cf. Fig. 18). Pollen with a round amb may be described as circular, and with respect to the relationship of apertures to the amb may be termed circulaperturate. Tricolpate or tricolpate-derived pollen without a circular amb has either concave, convex, or straight amb sides. Such pollen with straight amb sides may be described as polygonal, while pollen with concave or convex amb sides may be termed constricted-polygonal. Aperture location with respect to amb sides particularly may be an important phylogenetic character. In this regard polygonal pollen may be either angulaperturate with apertures situated in the angles of the amb sides or planaperturate with apertures situated at the mid-points of the amb sides. Constricted-polygonal pollen may be either lanceaperturate with apertures situated in the middle of the projecting parts of the concave amb sides or sinuaperturate with apertures situated in the sinuses of the concave amb sides. If constricted-polygonal pollen is deeply lobate with convex amb sides and the apertures are situated in the indentations between the lobes of the amb, the pollen may be described as fossaperturate.

Evolution of Pollen Grain Shape.—As previously mentioned, pollen grain shape is largely correlated with aperture type, polarity, and symmetry. Monosulcate grains are usually boat-shaped, heteropolar, and bilateral, while colpate grains are generally globose, isopolar, and radiosymmetric. Inaperturate pollen is normally globose, apolar, and radially symmetrical. The primitive shape of angiosperm pollen grains is clearly boat-shaped, with globose pollen representing an advanced character-state. Within boat-shaped, monosulcate pollen there appears to be an evolutionary trend from elongate (Fig. 17A) to oblong

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sperical pollen (*Aristolochia grandiflora* Sw.; Aristolochiaceae); × ca. 1360.—E. Globose-oblate pollen (*Eupomatia laurina* R. Br.; Eupomatiaceae). Polar view; × ca. 1850.—F. Globose-prolate pollen (*Decaisnea fargesii* Franch; Lardizabalaceae). Equatorial view; × ca. 1620.

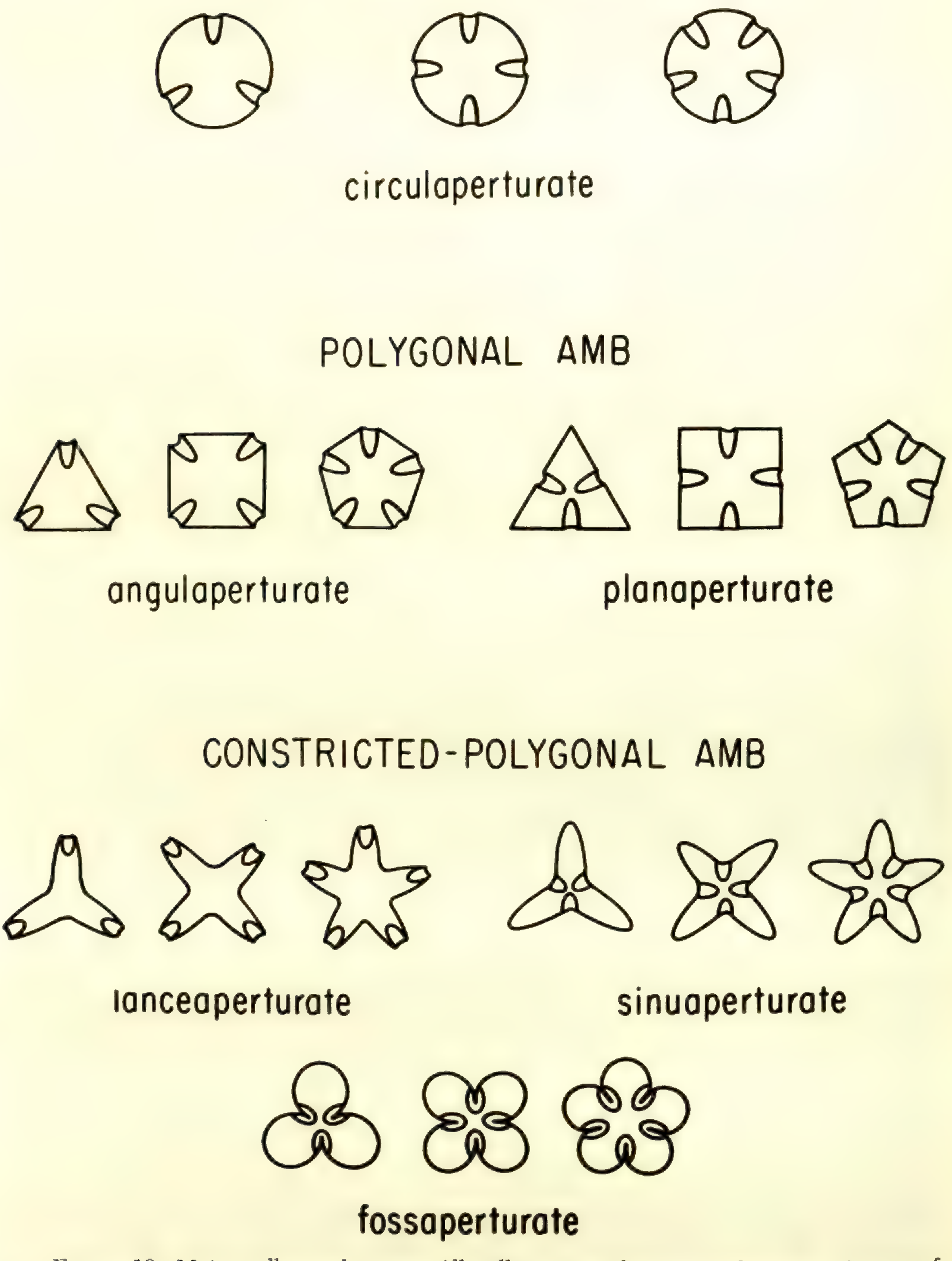

FIGURE 18. Major pollen amb types. All pollen grains shown in polar view. See text for discussion.

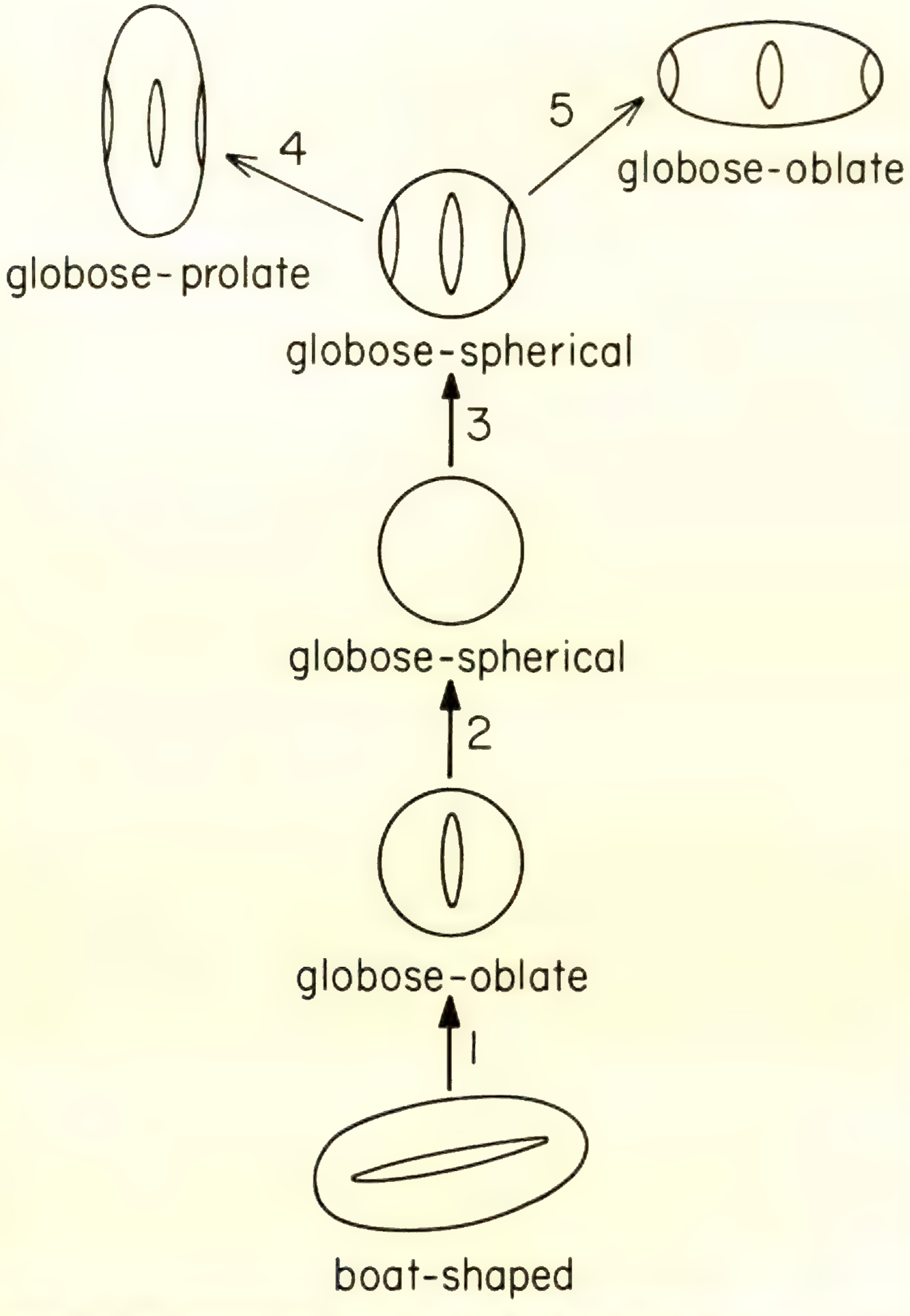

FIGURE 19. Major evolutionary trends in the shape of angiosperm pollen. Boat-shaped and globose-oblate monosulcate pollen shown in polar view; globose-spherical, globose-prolate, and globose-oblate tricolpate pollen shown in equatorial view. See text for discussion.

(Fig. 17B) to elliptic (Fig. 17C). Globose-spherical, inaperturate pollen appears to have developed from boat-shaped-elliptic pollen, generally via a more or less globose-oblate intermediate stage in which the pollen is still sulcate. Globose-spherical pollen in turn may develop into pollen which is either oblate again or prolate. The major evolutionary trends in the shape of angiosperm pollen are outlined in Fig. 19.

TABLE 5. Pollen size classes.

1) Minute grains	$< 10\mu$
2) Small grains	$10–24\mu$
3) Medium-sized grains	$25–49\mu$
4) Large grains	$50–99\mu$
5) Very large grains	$100–199\mu$
6) Gigantic grains	$\geqq 200\mu$

POLLEN GRAIN SIZE

The size of pollen grains may be somewhat affected by the method of preparation and hence can be a rather unstable character. Order of magnitude, based on defined size classes, is probably the single most useful measurement of whole pollen grains. The size classes listed in Table 5 (in part after Erdtman, 1945a), based on the length of the longest grain axis (exclusive of sculpturing elements in baculate, pilate, and echinate grains) have been adopted.

Angiosperm pollen exhibits a tremendous size range, from about 2 to 5μ in *Myosotis* (Boraginaceae) to over 300μ in *Cymbopetalum* of the Annonaceae. There are approximately a dozen angiosperm families that have species of some genera with pollen grains close to or greater than 200μ, including the Annonaceae (*Annona*, *Cymbopetalum*), Nyctaginaceae (*Acleisanthes*), Malvaceae (*Kokia*), Cucurbitaceae (*Cucurbita*), Onagraceae (*Oenothera*(= *Megapterium*)), Convolvulaceae (*Ipomoea*), Polemoniaceae (*Cobaea*), Dipsacaceae (*Morina*), Xyridaceae (*Orectanthe*), Musaceae (*Musa*), Zingiberaceae, and Marantaceae. The pollen of *Cymbopetalum odoratissimum* Barb. Rodr., with some individual grains as large as 350μ, probably represents the largest fixiform pollen grain in the flowering plants (Walker, 1971a). Mention must also be made of the nonfixiform, threadlike pollen of some marine angiosperms, which may be over 2000μ long, e.g., *Zostera* (Zosteraceae) and *Cymodocea* (Zannichelliaceae).

Evolution of Pollen Grain Size.—Primitive angiosperm pollen (i.e., the pollen of primitive taxa in the families Magnoliaceae, Degeneriaceae, Annonaceae, Austrobaileyaceae) falls largely between $50–99\mu$ in the large grain size class. It is therefore suggested that the primitive size of angiosperm pollen was in this size range. From large grains two different trends are apparent already within the subclass Magnoliidae—one trend toward even larger or gigantic grains (as evident within certain members of the family Annonaceae, cf. Walker, 1971b), and another trend toward smaller grains (cf. the small or minute grains in the two closely related families Saururaceae and Piperaceae). Pollen size is undoubtedly an easily reversible character and determination of the primitive size class for pollen of any particular taxon (order, family, etc.) must be based on correlation of pollen size with other characters of the taxon.

PALYNOLOGY AND THE TAKHTAJAN AND CRONQUIST SYSTEMS OF ANGIOSPERM CLASSIFICATION

In the following sections we will treat the 11 Takhtajan subclasses more or less in turn, considering what palynology indicates about their origins and

relationships, and noting distinctive trends within each subclass and the implications of such trends on relationships of their subgroups. Where the palynological trends are well established, in some cases on paleobotanical evidence, these comparisons will tend to confirm or negate the phylogenetic relationships and hence systematic groups proposed by Takhtajan and Cronquist; where the relationships are better established on non-palynological evidence, they may help demonstrate the direction of pollen-evolutionary trends, or indicate cases where trends break down or are reversed. Except in the Magnoliidae, Ranunculidae, and lower Hamamelididae, with which we are most familiar, we have relied heavily on Takhtajan (1966) and the classic work of Erdtman (1952) for information on the systematic distribution of pollen types; undoubtedly, a more complete and critical survey would modify some of our generalizations.

MAGNOLIIDAE

The Magnoliidae is putatively the most primitive subclass of dicotyledons in the Takhtajan and Cronquist systems of angiosperm classification. Palynology strongly supports this position in so much as the most primitive type of angiosperm pollen, viz., monosulcate and monosulcate-derived pollen, is restricted among dicotyledons solely to members of this subclass. Monosulcate pollen itself occurs in 15 families of the Magnoliidae (Magnoliaceae, Degeneriaceae, Himantandraceae, Annonaceae, Canellaceae, Myristicaceae, Austrobaileyaceae, Amborellaceae, Aristolochiaceae, Chloranthaceae, Lactoridaceae, Saururaceae, Piperaceae, Nymphaeaceae, and Cabombaceae), and represents the only known aperture type (exclusive of occasional trichotomosulcate variants) in eight of these families (Magnoliaceae, Degeneriaceae, Himantandraceae, Canellaceae, Austrobaileyaceae, Lactoridaceae, Saururaceae, and Cabombaceae). However, monosulcate pollen which has a particularly "gymnospermous" aspect (i.e., is strongly heteropolar, bilaterally symmetrical, and boat-shaped) is restricted largely to the families Magnoliaceae, Degeneriaceae, and Annonaceae. The polycolpate/polyporate pollen in the Chloranthaceae (*Hedyosmum* spp., *Chloranthus*) and Aristolochiaceae (*Asarum* spp.) is unique among colpate pollen in being monosulcate-derived, while tricolpate or tricolpate-derived pollen itself occurs in the families Illiciaceae, Schisandraceae, and Nelumbonaceae.

Within the Magnoliidae, atectate pollen (i.e., primitively columellaless pollen) occurs in the families Magnoliaceae, Degeneriaceae, Eupomatiaceae, and Annonaceae, and may be present also in the Himantandraceae and some Nymphaeaceae. Most magnoliid pollen, however, is tectate (cf. Walker, 1974b). Taxa within the subclass that have semitectate pollen include a few Annonaceae (e.g., *Deeringothamnus*), some Myristicaceae (e.g., *Myristica*, *Osteophloem*, *Horsfieldia* spp.), all Winteraceae, Illiciaceae, and Schisandraceae, *Saruma* of the Aristolochiaceae, and some Chloranthaceae (*Chloranthus* spp., *Sarcandra*). Intectate pollen is very rare, occurring as far as is known in only two genera of the Annonaceae (*Ophrypetalum*, *Trigynaea*) and in some species of the myristicaceous genus *Horsfieldia*.

Takhtajan's order Magnoliales (with one exception) appears to represent a

close-knit group palynologically. Its members are held together by a number of pollen characters, although in some instances these common pollen characters may occur only in the primitive taxa within a particular family. Unifying palynological characteristics of this order are seen in pollen which is frequently monosulcate, atectate to tectate-imperforate, more or less psilate, large to medium-sized, solitary, heteropolar, bilateral to isobilateral, and boat-shaped to globose-oblate. The greatest pollen diversity in the subclass occurs in the magnolialean family Annonaceae, where pollen characters have proved especially useful for infrafamilial classification (cf. Walker, 1971b, 1972a). The similar medium-sized, more or less psilate, tectate-imperforate, globose-oblate, isobilateral monosulcate pollen which occurs in certain members of the families Canellaceae and Myristicaceae (e.g., *Warburgia* and *Dialyanthera*) seems indicative of a close relationship between these two families. Although pollen of the Eupomatiaceae is atectate, psilate, medium-sized, and solitary, it departs somewhat from that of other members of the order in being zonasulculate. The family Winteraceae, however, is completely disharmonious within the order in having anaulcerate, semitectate-reticulate, radiosymmetric, globose-spherical pollen which is in permanent tetrahedral tetrads. In terms of its semitectate-reticulate exine structure, winteraceous pollen more closely resembles pollen of the Illiciaceae-Schisandraceae. Palynological data strongly oppose Hutchinson's (1964) placement of *Degeneria* (with its anasulcate, atectate, bilateral, boat-shaped, solitary pollen) within the Winteraceae.

The order Laurales, sensu Takhtajan, by contrast is characterized largely by inaperturate, more or less sculptured, apolar, radiosymmetric, globose-spherical pollen grains (e.g., most Monimiaceae, and all Hernandiaceae, Gomortegaceae, Lauraceae, and Gyrocarpaceae). Interestingly, the otherwise primitive Austrobaileyaceae possess well-developed monosulcate pollen, and pollen grains of the primitively vesselless Amborellaceae may be either inaperturate or sulcoidate. Pollen of the Calycanthaceae, Atherospermataceae, and the newly described Idiospermaceae (cf. Blake, 1972) is disulculate. The echinate pollen of *Peumus* in the Monimiaceae shows a resemblance to the echinate pollen of the Hernandiaceae in that spines which occur on the pollen in both of these families are made up of separate, cable-like subunits. On the other hand, a different type of echinate pollen characterizes the families Gomortegaceae, Lauraceae, and Gyrocarpaceae, which appear to represent a close-knit group. The families Chloranthaceae and Lactoridaceae show little or no relationship palynologically to the rest of the order. Although pollen of *Lactoris* is in permanent tetrads, it appears to have little else in common with pollen of the Winteraceae. Pollen morphology supports the naturalness of the Piperales, sensu Takhtajan, since both the Saururaceae and Piperaceae have distinct, small to minute, monosulcate pollen which does not occur elsewhere in the subclass. Pollen morphology of the Aristolochiaceae supports its isolated position in a monotypic order. The great diversity of pollen types which characterizes the genera of Nymphaeales supports the idea that this is a very old order and also supports the separation of Nymphaeaceae, sensu lato, into a number of separate families. For example, most members of the Nymphaeaceae, sensu stricto, possess a distinctive aperture (a zonasulculus) found elsewhere in the subclass only in the Eupomatiaceae.

The pollen morphology of some magnoliid families is indicative of relationships with other dicotyledonous subclasses. For example, there is a strong similarity in pollen size, sculpturing, exine stratification, and apertures between pollen of the Chloranthaceae and certain "lower" Hamamelididae (e.g., Cercidiphyllaceae, Trochodendraceae, Tetracentraceae, Eupteleaceae). Some ranunculid pollen (e.g., that of the menispermaceous genus *Tinospora*) exhibits great similarity to the pollen of the Illiciaceae-Schisandraceae, which appear to represent a connecting link between magnoliid and ranunculid dicots, cf. placement of these two families by Cronquist (1968) and Takhtajan (1969). Pollen grains of both *Tinospora* and *Schisandra* show similarity in being semitectate-reticulate and polarly syncolpate, and pollen of these two genera possesses the same peculiar linear median thickening in the colpi. For further details on the pollen of the subclass Magnoliidae, see Walker (1974b, 1974c, 1975, 1976).

MONOCOTYLEDONAE

Like the Magnoliidae, the monocotyledons are a basically monosulcate group, and they illustrate many of the same trends and problems we have already considered. Although certain monosulcate-derived aperture conditions are more prevalent among monocots than in magnoliid dicots, there are some members of both groups which retain the essentially gymnospermous boat-shaped monosulcate type which is believed on both comparative and fossil evidence to be basic to angiosperms as a whole. Hence we must look at features other than aperture condition for any of the distinctive specializations which we might expect if the monocots represent a major monophyletic group within the angiosperms. One such specialization may be a tendency for open-reticulate or semitectate exine structure on most of the grain surface with finer tectate or tectate-perforate structure at the "bow" and "stern" and near the sulcus margins. Such pollen is found among some of the oldest angiospermous monosulcates of the Lower Cretaceous—being described under the form-genera *Retimonocolpites* and *Liliacidites* (Doyle, 1973; Wolfe et al., this symposium)—and is found also in representatives of all four monocot subclasses, including some of their putatively more primitive members (e.g., Butomaceae, Liliales, Bromeliaceae, Araceae, Palmae), but not in magnoliid dicots. This distribution is consistent with the hypothesis (suggested by Doyle, 1973) that the *Liliacidites*-type is basic for the monocotyledons, although the fact that other monocots have more uniformly tectate exines means that further comparative studies are needed.

Alismatidae.—In the generally aquatic monocot subclass Alismatidae, monosulcate pollen of the *Liliacidites*-type is found in the genus *Butomus*, which is often considered the most primitive member of the subclass. Most other Alismatidae are more specialized in their pollen morphology, in keeping with the other specializations which rule them out as the direct ancestral complex for the monocots (e.g., seeds without endosperm, trinucleate pollen: cf. Cronquist, 1968; Takhtajan, 1969). All members of the Alismatales except *Butomus* are polyforate, with 4–20 scattered pore-like apertures. The Hydrocharitales and Najadales show loosely correlated tendencies for loss of the sulcus (still seen in some Hydrocharitaceae and Aponogetonaceae) and reduction in sculpture, so that most of them are

inaperturate, often with thin, finely spinulose exines, analogous to those noted in the Laurales. The culmination of this trend is apparently seen in the marine members of these orders: here the pollen consists of flexible, "non-fixiform" threads up to 2 mm long, whose walls consist entirely of cellulosic intine. Since this specialization occurs in marine members of both Hydrocharitales (Thalassioideae and Halophiloideae) and Najadales (Zosteraceae, Posidoniaceae, Cymodoceaceae), it presumably represents an independent, convergent adaptation to marine conditions.

Liliidae.—The subclass Liliidae includes a much larger proportion of members with the primitive monosulcate condition, many with the *Liliacidites*-type of sculpture differentiation (e.g., Liliaceae, Amaryllidaceae, Stemonaceae). Other monosulcate-derived aperture types seen in the Liliales and Iridales are trichotomosulcate, operculate-monosulcate, disulculate, and diulculate. Although the coexistence (e.g., in Agavaceae) of operculate and zonasulculate types suggests a mode of origin for zonasulcates similar to that postulated in the Nymphaeaceae (see above), the elongate shape of the diulculates (e.g., *Colchicum*), with the ulculi located at the ends of the grain, suggests that the two apertures may represent cut-off ends of the sulcus. Other Liliales show a reduction trend leading to inaperturate, often finely spinulose grains (e.g., Smilacaceae), while a few show the unusual spiraperturate condition (Aphyllanthaceae, some Xanthorrhoeaceae), seen also in the commelinid family Eriocaulaceae.

The Zingiberales, which Cronquist places in the Commelinidae and Takhtajan in the Liliidae, illustrate an extreme case of the reduction trend: in most of them, the exine is reduced to small, acetolysis-resistant spinules, and the intine is thickened proportionately (cf. Skvarla & Rowley, 1970). There are only rare vestiges of the single distal aperture (Heliconiaceae, *Zingiber*; Kuprianova, 1948); hence we would suggest that the polyforate to spiraperturate condition seen in Costaceae represents secondary origin of apertures. Finally, the Orchidaceae show a striking trend, analogous to that seen in the Apocynaceae and Asclepiadaceae among the dicots, from single grains (sometimes reticulate and monosulcate) to tetrads, polyads, massulae, and highly specialized pollinia consisting of the entire contents of an anther locule.

Commelinidae.—The most striking trend in the subclass Commelinidae, apparently tied to the shift there to wind pollination, leads from monosulcate to the monoulcerate (monoporate) condition seen in grasses. Although Cronquist (1968) groups the grasses and sedges in the order Cyperales, palynology favors Takhtajan's (1969) interpretation of the two groups as more distantly related, the grasses being derived from the Restionales and the sedges from the Juncales. Monosulcate pollen occurs in the Bromeliales and Commelinales, but in the Restionales we find a transitional series from irregular-aperturate (Centrolepidaceae, some Restionaceae) to essentially graminoid monoulcerate grains (Flagellariaceae, other Restionaceae; cf. Chanda, 1966). Most sedges, on the other hand, have very peculiar asymmetrical, ovoid grains with one or four blotchy apertures, which are referred to as pseudomonads or cryptotetrads, since each grain is derived from one pollen mother cell by degeneration of three of the haploid nuclei (cf. Cranwell, 1953; Dunbar, 1973). This is readily imagined as a specialization

from the situation in the Juncaceae, which have ulceroidate grains united in permanent tetrads.

Arecidae.—The last monocot subclass, the Arecidae, shows most of the aperture and exine structure trends exhibited by the other monosulcate groups, as well as some of its own. Sowunmi (1968, 1972) and Thanikaimoni (1970b) have inferred a variety of aperture trends in the palms, from the widespread, often reticulate monosulcate condition to trichotomosulcate, ulcerate, and, by extension of the furrow all around the grain, to the zonasulcate condition in the unique, spiny grains of *Nypa*. The two furrows of the Lepidocaryoideae are postulated to have arisen either by constriction of the middle of an extended distal sulcus (Thanikaimoni, 1970b), or of the two polar portions of a complete zonasulcus of the *Nypa* type (Sowunmi, 1968); in either case, the furrows must be longitudinal and hence analogous to the colpi of higher (dicolpate) dicotyledons rather than the sulculi of many Magnoliidae. Diporate grains may have arisen either by contraction of such colpi (Thanikaimoni) or isolation of the ends of a sulcus (Sowunmi).

The Araceae show both *Liliacidites*-type monosulcates and still more of the basic monosulcate-derived types, including "ephedroid" striate monosulcates, spinulose inaperturates, and polyforates (cf. Thanikaimoni, 1969). Spinulose grains with a reduced aperture occur in the Lemnaceae, consistent with their postulated derivation from the Araceae. Finally, the characteristic ulcerate, usually reticulate grains of Pandanaceae, Sparganiaceae, and Typhaceae, similar to those in some Cyclanthaceae, support Takhtajan's (1969) grouping of these three families in the Arecidae.

NON-MAGNOLIID DICOTYLEDONAE

With the problematical exception of *Nelumbo* (which Takhtajan in fact refers to the Ranunculidae), all the groups considered so far have had monosulcate and monosulcate-derived pollen types. In contrast, the remaining six subclasses of non-magnoliid dicots have exclusively tricolpate and tricolpate-derived pollen types. Unfortunately, neither modern nor fossil evidence indicate clearly how tricolpate pollen originated. The two most commonly postulated intermediates between the monosulcate and tricolpate conditions are trichotomosulcate (giving rise to tricolpate by isolation of the three arms of the furrow: Straka, 1963; Wilson, 1964) and inaperturate (with colpi arising *de novo*: Muller, 1970; Walker, 1974c). Difficulties with the trichotomosulcate hypothesis include the rarity of trichotomosulcates among possibly related magnoliid dicot groups, and the difference in orientation (with reference to the other grains in the meiotic tetrad) of the three arms in trichotomosulcate grains (according to "Garside's law," meeting in four groups of three) and the three colpi of tricolpates (according to "Fischer's law," meeting in six groups of two) (cf. Erdtman, 1969). However, the extinct hypothetical ancestors of the tricolpates need not have had the same orientation as in those modern trichotomosulcates where it is known (mostly monocots). A strong case has been made for the *de novo* origin of several equatorial apertures from inaperturate ancestors in the Chloranthaceae and Aristolochiaceae; again, it is uncertain whether analogies can be drawn to the situation in non-magnoliid dicots, with their regularly three-fold symmetry. Furthermore, it is not clear whether the

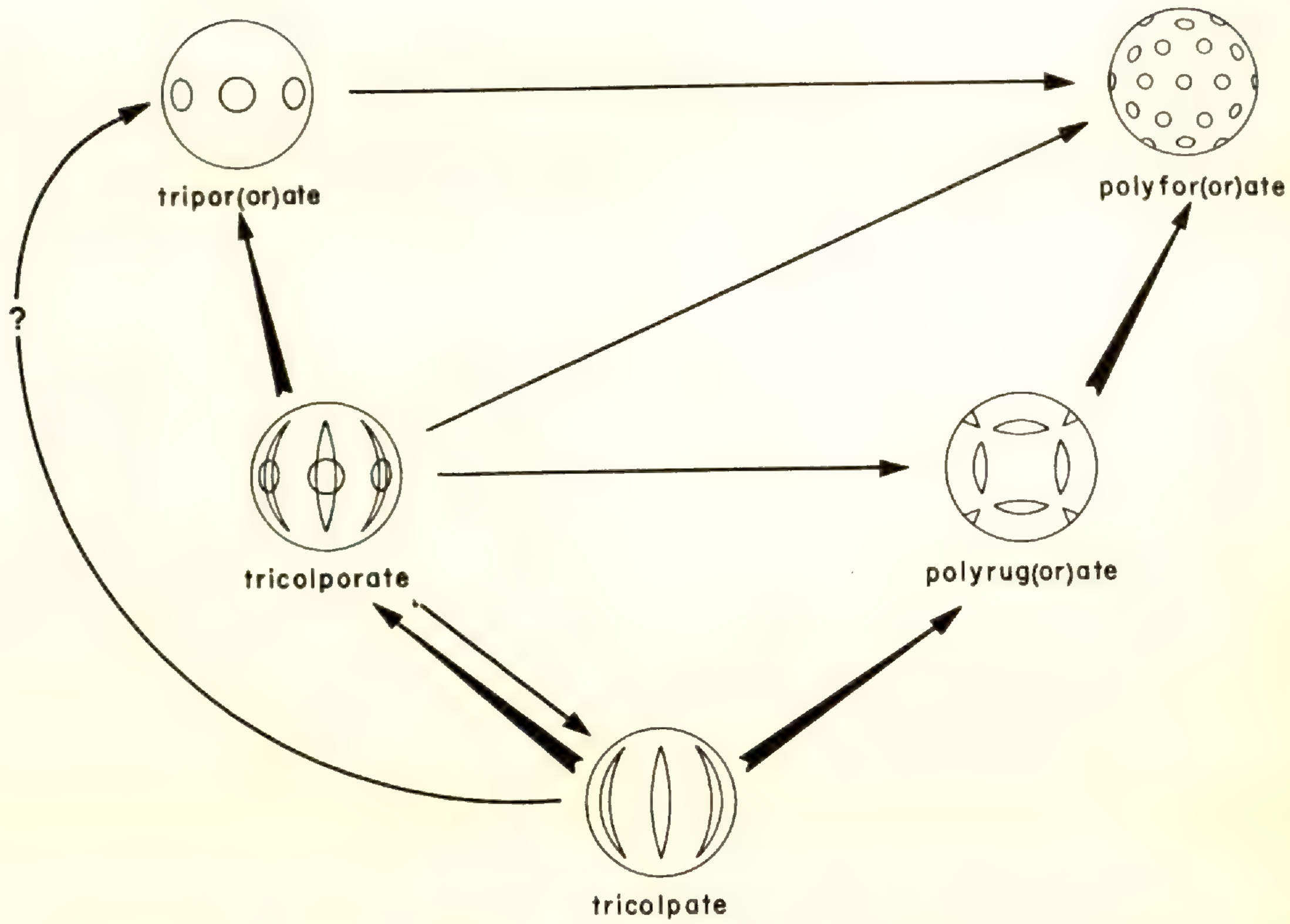

FIGURE 20. Principal evolutionary transformations in pollen aperture condition in non-magnoliid dicotyledons. Thick arrows indicate major trends, fine arrows less important ones. Parentheses indicate cases where ora may or may not be present, depending on the group in question. See text for discussion.

tricolpate condition arose once or several times, and hence whether the six non-magnoliid subclasses form a monophyletic group within the dicots, or simply a grade or level of advancement (cf. Wolfe et al., this symposium). Studies of both modern and fossil tricolpates and their possible non-tricolpate relatives are desirable to test hypotheses on the origin of tricolpates, and especially to identify the one or more monosulcate ancestors or "sister groups" of the tricolpate subclasses.

Among the trends affecting tricolpate groups (Fig. 20), probably the most important is the origin of compound apertures, resulting in the tricolporate condition, with round or variously elongate thin areas (ora) at the centers of the colpi. Tricolporoidates, where the ora are poorly defined (oroids), represent an intermediate condition. Tricolporate grains are in fact numerically dominant in the modern dicot flora. This trend is directly documented from the Cretaceous fossil record (Doyle, 1969; Muller, 1970; Wolfe et al., this symposium), quite independently of the comparative morphological evidence on which it was originally postulated (e.g., by Takhtajan, 1959). In a few groups, there is evidence for apparent reversal of the main tricolpate-tricolporate trend by reduction of the ora, resulting in secondarily simple apertures. A well-documented trend runs from tricolpate to polyrugate, with many furrows or rugae scattered globally over the surface of the grain, and by shortening of the rugae to polyforate,

with numerous scattered pore-like apertures or foramina. Polyrug(or)ate and polyfor(or)ate grains may also be derived from compound-aperturate ancestors.

The triporate and tripororate conditions, with respectively simple and compound round equatorial apertures, represent still additional specializations from the tricolpate condition. It is quite uncertain whether triporate grains have ever arisen directly from tricolpate ancestors by shortening of simple colpi. A few morphological series indicate that simple triporates may arise from tricolporates by a gradual in-place-disappearance of the colpi (i.e., via tricolpoidorate intermediates). In most cases, however, there is evidence that triporates arose from tricolporates by shortening of the furrows (i.e., via brevitricolporate intermediates); here the resulting forms are often clearly pororate. Subsequent reduction could lead to apparently simple pores, as in the minute grains of many Urticales.

Ranunculidae.—Within the first tricolpate-derived subclass, the Ranunculidae, many Ranunculales (some Ranunculaceae, Lardizabalaceae, Menispermaceae, Berberidaceae sensu lato) retain simple, often finely reticulate tricolpate pollen of the type first seen in the Lower Cretaceous fossil record (cf. Doyle, 1969; Muller, 1970; Wolfe et al., this symposium). Although a few Menispermaceae (and Lardizabalaceae?) are tricolporate, most Ranunculidae have simple apertures; in fact, the compound (tricolporate) apertures of *Paeonia* are one of the reasons for believing that this genus belongs neither in the Ranunculaceae nor the Ranunculidae, but rather in the Dilleniidae. Especially in the Ranunculaceae, there is a series leading from tricolpate through polyrugate to polyforate grains, with a precisely defined geometric relationship of the apertures ("successiformie" of Van Campo, 1967), and often with granulate aperture membranes and small supratectal spinules. Occurrence of the same trends in the Papaverales and the Caryophyllidae (see below) supports the hypothesis that these two groups are derived from Ranunculales (Van Campo, 1967; Roland, 1971).

Problematical aperture situations are seen in the Illiciaceae and Schisandraceae, considered to constitute the most primitive order (Illiciales) of the Ranunculidae by Takhtajan (1969), but retained in the Magnoliales by Cronquist (1968). *Illicium* is reticulate and tricolpate, but the three colpi meet at the poles (syncolpate). *Kadsura* and most *Schisandra* species are hexacolpate, with three short colpi alternating with three which join at one pole, but *Schisandra grandiflora* has just three colpi which join at one pole, presumably corresponding to the three fused colpi of the other species. All three types may represent specializations from a simple tricolpate condition, but an intriguing possibility is that the S. *grandiflora* type represents a unique survivor of the three-armed intermediate postulated by the trichotomosulcate theory.

Hamamelididae.—Reticulate tricolpate pollen, often with granulate colpus membranes, is also retained by some of the putatively more primitive members of the subclass Hamamelididae, such as *Trochodendron*, *Tetracentron*, *Cercidiphyllum* (with somewhat anomalous ill-defined apertures), *Platanus*, and most Hamamelidaceae. A few Hamamelididae, such as *Euptelea*, some Hamamelidaceae (*Chunia*, *Sycopsis*), and occasionally *Platanus*, vary from tricolpate to hexarugate. In marked contrast, most of the "higher" Hamamelididae or classic

"Amentiferae," i.e., Betulaceae, Myricaceae, *Casuarina*, *Rhoiptelea*, Juglandaceae, Ulmaceae, Moraceae, Cannabaceae, and Urticaceae, have much more advanced triporate or derived (diporate, polyporate) pollen types. Although some Hamamelidaceae (*Liquidambar*, *Altingia*) have pores, these are simple, presumably rugate-derived foramina, whereas most porate Amentiferae have clearly compound apertures (i.e., they are actually pororate). This suggests that the triporate Amentiferae were not derived directly from simple-aperturate forms (as in all Hamamelidales except *Rhodoleia*), but rather from tricolporate ancestors by shortening of the colpi. In some Amentiferae, such as *Rhoiptelea*, a presumed primitive relative of the Juglandaceae, and *Planera* (Ulmaceae), somewhat misleadingly described by Erdtman (1952) as colpate, the outer apertures are in fact short colpi. Furthermore, Upper Cretaceous fossil sequences show apparently transitional series from triangular tricolporates of a type more characteristic of Rosidae than Hamamelidales (see below), through triangular triporates of the so-called Normapolles complex (many of which have features, such as arci, suggestive of *Rhoiptelea*, Betulaceae, Ulmaceae, etc.), to essentially amentiferous types (Góczán et al., 1967; Doyle, 1969; Muller, 1970; Wolfe et al., this symposium). Tricolporate grains do occur in some Hamamelididae, such as *Rhodoleia*, Fagaceae, *Eucommia* (with a peculiar asymmetry in the length of the colpi), *Barbeya*, and *Leitneria*, but except perhaps for *Trigonobalanus* in the Fagaceae (Erdtman, 1967), they show few tendencies toward the triangular tricolporate intermediate condition inferred from the fossil record. Finally, the higher Hamamelididae investigated differ from the Hamamelidales in having granulate rather than columellate infratectal exine structure, but such structure is found in some Rosidae (Van Campo & Lugardon, 1973).

Caryophyllidae.—Whereas palynology thus casts some doubt on the naturalness of the Hamamelididae, it strongly confirms the unity of the subclass Caryophyllidae, especially the core orders Caryophyllales and Polygonales, and their postulated derivation from the Ranunculidae. Within several families (Phytolaccaceae, Nyctaginaceae, Cactaceae, Portulacaceae, and Caryophyllaceae) we see both the same type of tricolpate pollen with granulate colpus membranes and supratectal spinules as in the Ranunculaceae, and the same trend from tricolpate through polyrugate to polyforate (cf. Van Campo, 1967; Roland, 1971). In keeping with their high degree of specialization and postulated close relationship, the Chenopodiaceae and Amaranthaceae are exclusively polyforate. Finally, the Polygonaceae show sculpture and aperture trends comparable to those in the Caryophyllales, but they are more specialized in having compound apertures. It may be noted that there is no palynological indication of the heterogeneity of the Caryophyllidae inferred from chemical data (cf. Fairbrothers et al., this symposium).

Comparison of Dilleniidae and Rosidae.—Most of the orders in the next two subclasses, Dilleniidae and Rosidae, appear to be basically tricolporate rather than tricolpate, and hence in this character more specialized than the preceding subclasses (except "higher" Hamamelididae or "Amentiferae"). A few members have tricolpate pollen, but in most cases their relatively advanced position as inferred from other characters and comparisons with related groups suggest that

this is a result of secondary reduction of ora from tricolporate ancestors, resulting in an apparent reversal of the tricolpate-tricolporate trend (see below). The most convincing examples of retention of the primitive tricolpate condition are seen in some Dilleniaceae, where *Hibbertia* and several other genera have reticulate tricolpate pollen associated with putatively primitive non-palynological features, while others (*Davilla*, *Tetracera*, etc.) are tricolporate (Dickison, 1967).

Although there are some distinctive trends which tend to unify and relate various orders within the Dilleniidae and Rosidae, the more primitive pollen types and many of the most basic trends are so similar that palynological evidence is ambiguous on whether the two subclasses as a whole represent two such distinct major groups as indicated by the Takhtajan and Cronquist systems. One of the most important of these parallel trends concerns size and the degree of differentiation of exine and aperture structure. Some members have small, thin-walled, psilate or finely reticulate tricolporoidate pollen, whereas others have larger, thicker-walled, and sometimes highly sculptured pollen with well-developed ora, thickened colpus margins, and other endexinal specializations. That this reflects an *elaboration* trend was originally inferred from comparative studies of modern tricolporate groups (Van Campo, 1946, 1966; Dahl, 1952; Muller, 1969a), and is confirmed by observation of a stratigraphic elaboration trend among the first tricolporates of the early Upper Cretaceous (cf. Muller, 1970; Doyle, 1973; Wolfe et al., this symposium). Curiously, this appears to represent reversal of a still earlier size and sculpture reduction trend seen among their presumed late Lower Cretaceous tricolpate ancestors (Doyle, 1969). In any case, caution must be used in generalizing these trends to modern groups: while the fossil evidence may indicate that all large tricolporates are more advanced than at least some small tricolporoidates, small size cannot be interpreted so simply, since secondary decrease in size is both easy to imagine and strongly inferred in some cases (e.g., *Myosotis*).

Dilleniidae.—Within the Dilleniidae, most of the more generalized tricolporate forms would be difficult to exclude from the Rosidae; they differ from the latter more on the absence of the "rosid" shape and aperture trends discussed below. An area in which to seek more positive dilleniid specializations may be comparative developmental studies of exine structure, e.g., to determine whether other types in the subclass can be interpreted as variations on the "tilioid" type, with a reticulum formed of an undulate tectum, cited by Van Campo & Lugardon (1973) as seen in the "Dilleniales" (Dipterocarpaceae) and Malvales (Van Campo, personal communication).

Groups of Dilleniidae with small, relatively unsculptured tricolpor(oid)ate grains include many Ochnaceae (Muller, 1969a), the subfamily Ternstroemioideae of the Theaceae (Keng, 1962), Marcgraviaceae, Hypericaceae, and Elatinaceae within the Theales; Lacistemataceae, many Flacourtiaceae (usually finely reticulate rather than psilate), Datiscaceae, and Begoniaceae in the Violales (sensu lato); Cyrillaceae and Saurauiaceae in the Ericales; and Elaeocarpaceae in the Malvales. Groups with more advanced, larger, thicker-walled tricolporate pollen include *Ochna* and a few other Ochnaceae, the subfamily Camellioideae in the Theaceae, Dipterocarpaceae, Quiinaceae, and Guttiferae (often with very

thick exines) in the Theales; Violaceae, Bixaceae, Cistaceae, and those families considered advanced members of the Violales by Cronquist but segregated as the Passiflorales by Takhtajan; and many Tiliaceae and some Sterculiaceae in the Malvales. These characters agree roughly with the relative advancement of these families in the Takhtajan and Cronquist systems.

The reticulate, prolate tricolporoidate pollen of *Salix* (placed in the Amentiferae in the Englerian system) is more consistent with Takhtajan and Cronquist's derivation of the Salicaceae (including also the inaperturate *Populus*) from the Violales, specifically the Flacourtiaceae. However, since both some *Salix* species and the putatively related Frankeniaceae and Tamaricaceae are described as tricolpate, this derivation requires reversal of the major tricolpate-tricolporate trend. Similarly, in the Capparales the Cruciferae are described as tricolpate (occasionally hexacolpate, etc.), whereas the putatively more primitive Capparaceae, Tovariaceae, and Moringaceae have generally tricolporate pollen. Other candidates for reversion are seen in the Primulales, where the Myrsinaceae and Theophrastaceae are usually tricolporate, while the Primulaceae include tricolpates as well as syncolpates and pollen with increased numbers of apertures.

Several dilleniid orders exemplify peculiar pollen types and trends, some of which have no close analogs in the Rosidae. Within the Ericales, the Saurauiaceae, Actinidiaceae, Clethraceae, and Cyrillaceae have simple, relatively smooth tricolporate grains (consistent with their postulated transitional relationship to the Theales), but most Ericaceae, Pyrolaceae, and Empetraceae have permanent tetrads, while the Epacridaceae have tetrads consisting of one viable and three abortive grains, representing an unusual mode of reversion to functional monads. The Malvales are very diverse palynologically, but the existence of intermediate conditions and "reticulate" similarities between families supports the concept that they form a natural group. In agreement with their postulated primitive position, the Elaeocarpaceae have small, smooth, tricolporoidate pollen. Among the more specialized conditions in the order are oblate triporate or brevicolporate grains in Bombacaceae and some Tiliaceae (e.g., *Tilia*) and Sterculiaceae (with the apertures on the flat or concave sides of the grains, rather than at the angles as in many Rosidae), and large polyforate grains with prominent spines in Malvaceae and some Sterculiaceae. The fact that the Sterculiaceae include both generalized tricolporates and most of the advanced types found in the other families suggests they may be a paraphyletic (grade) taxon consisting of primitive relatives (sister-groups) of the higher groups. The Ebenales also show a diversity of relatively advanced pollen types: fairly large tricolporates in Styracaceae and Ebenaceae, thick-walled tetracolporates in Sapotaceae, and oblate-triangular brevitricolporate to triporate grains (more suggestive of Rosidae) in Symplocaceae. Here the connections are less evident than in the Malvales, and further palynological study might be of interest in evaluating the naturalness of the group and its postulated derivation from the Theales.

Rosidae.—The same size and sculpture elaboration trend as seen in the Dilleniidae can be seen in the Rosidae. Small, finely reticulate or psilate tricolporoidate pollen is especially common in the Saxifragales (Cunoniaceae, Davidsoniaceae, Escalloniaceae, Hydrangeaceae, Crassulaceae, and Saxifraga-

ceae sensu stricto), in keeping with the postulated basal position of this order, and in some Araliaceae, Cornaceae (e.g., *Curtisia*), and Celastrales (e.g., Phelliniaceae, some Celastraceae). Larger tricolporate pollen, often with elaborate colpus margins and ora, is typical of most Pittosporaceae, Rosaceae, legumes (except Mimosaceae: see below), Rutales, Sapindales, Cornales (e.g., *Nyssa*, *Cornus*, *Mastixia*), Rhamnaceae, Vitaceae, Celastrales, and Oleaceae.

Even within the most primitive of these groups (e.g., Cunoniaceae, Saxifragaceae), certain tendencies are seen which are widespread throughout the Rosidae but very rare in the Dilleniidae, especially oblate-triangular grains with apertures at the angles (breviaxy, discussed by Van Campo, 1966), syncolpy, reduction to the dicolp(or)ate condition, and striate sculpture. Groups with oblate-triangular, angulaperturate grains, occasionally syncolpate, include many Cunoniaceae, Araliaceae, Myrtaceae (see below), Burseraceae, Simaroubaceae, Sapindaceae, Humiriaceae, Vochysiaceae, Nyssaceae, Icacinaceae and other Celastrales, Rhamnaceae, Vitaceae, and Elaeagnaceae. The prevalence of this trend to triangular shape and shortening of apertures in the Rosidae has been mentioned above as evidence that the triporate "Amentiferae" or higher Hamamelididae are more closely related to the Rosidae than to the Hamamelidales (cf. also Wolfe et al., this symposium). Dicolporate grains, often extremely small, are seen in Cunoniaceae, Eucryphiaceae, Myrtaceae, Crypteroniaceae (placed in Saxifragales by Takhtajan, Myrtales by Cronquist), and Corynocarpaceae (Celastrales according to Takhtajan; palynology hence contradicts Cronquist's placement of this family in the Ranunculales). Striate grains are common in Saxifragaceae, Crassulaceae, Rosaceae, Caesalpiniaceae, Anacardiaceae, Burseraceae, Simaroubaceae, Rutaceae, Cneoraceae, Aceraceae, Hippocastanaceae, Melianthaceae, Vochysiaceae, Krameriaceae, Loranthaceae, etc.

The Myrtales and Santalales show what may be interpreted as special elaboration of these "rosid" trends. Interestingly, the Lythraceae and Olacaceae, considered the most primitive members of their respective orders by Takhtajan and Cronquist, bear much the same palynological relationship to the other members as do the Sterculiaceae to the other Malvales.

The Myrtales include not only a few members with prolate tricolporate pollen (Punicaceae, some Lythraceae, Rhizophoraceae), but also a variety of other types: triangular tricolporates, often syncolpate, in Myrtaceae and Lythraceae (associated with striate sculpture in *Cuphea*); prolate triporates (resulting from disappearance in place rather than shortening of colpi ?) in Sonneratiaceae and some Lythraceae (the origin of the large, sculptured grains of *Sonneratia* from smaller, more lythraceous precursors is documented by the fossil record: Muller, 1969b); large, thick-walled triangular triporates in Onagraceae; and forms with three colporate apertures alternating with three (*de novo* ?) pseudocolpi in Combretaceae, Melastomataceae, Penaeaceae, and some Lythraceae and Oliniaceae. It may be noted that these "rosid" palynological trends contrast with "dilleniid" features in the leaf architecture of the Myrtales (Hickey & Wolfe, this symposium); further study is desirable to determine which set of similarities are the result of convergence.

In the Santalales, the vegetative trend to parasitism is rivalled by equally

bizarre trends in pollen morphology. Relatively unspecialized triangular tricolporates exist in some Olacaceae, Opiliaceae, and Octoknemaceae; syncolpates (often heteropolar) in other Olacaceae, Santalaceae, and Loranthaceae. The *Anacolosa*-type (Olacaceae), with three pores located on each hemisphere of an oblate triangular grain, may be related to the latter type. Finally, a few Olacaceae have strikingly "proteaceous" triangular triporate grains, possibly providing a clue to the relationships of the otherwise enigmatic Proteaceae, although similar types are also seen in the Icacinaceae (Celastrales) (cf. Erdtman, 1952; Muller, 1970).

Several other unusual or problematical trends seen in the Rosidae may be mentioned. Multiplication of the number of equatorial colporate apertures has occurred in several groups, with the Bruniaceae and Polygalaceae (up to 28-colporate) representing the most extreme cases. Candidates for reversal of the tricolpate-tricolporate trend are seen in the Linales and Geraniales: the woody members (many Humiriaceae, Erythroxylaceae, Zygophyllaceae, etc.) tend to have tricolporate pollen, while some members of the more typically herbaceous families (Linaceae, Oxalidaceae, Geraniaceae) are described as tricolpate. Finally, among the legumes the Mimosaceae show a great array of tetrad and polyad types and peculiar, asymmetric porate grains apparently representing secondary monads. Other Mimosaceae (e.g., *Leucaena*, *Neptunia*, *Prosopis*) have more "normal" tricolporate monads suggesting links with the related Caesalpiniaceae and Papilionaceae; however, Guinet (1966, 1969) has shown that within *Leucaena* and other genera these tricolporate grains can be connected through asymmetric tricolporate forms to obvious secondary monads, suggesting that the compound condition may actually be primitive in the family.

The two most important cases in which the Takhtajan and Cronquist systems differ on whether a group should be placed in the Dilleniidae or Rosidae involve the Lecythidaceae (Rosidae, in fact Myrtales according to Takhtajan, Dilleniidae according to Cronquist) and the Euphorbiales (Dilleniidae near Malvales according to Takhtajan, Rosidae near Celastrales according to Cronquist). Unfortunately, palynology does not yet provide a clear-cut answer to either problem. In the Lecythidaceae, a partial series can be seen from tricolpate (tricolporate with lolongate ora ?) to the syncolpate *Planchonia*-type, with specialized grooves at the colpus margins and thickenings at the poles (Muller, 1972, 1973). The syncolpate condition might suggest connections with the Myrtales, though no really close analogs exist there. Similar grains also occur in the thealian family Caryocaraceae (Barth, 1966), but in either case the similarities must be at best parallelisms rather than true homologies, since the syncolpate trend occurs *within* the Lecythidaceae (cf. Muller, 1972, 1973). Palynology helps confirm the relationship postulated by Takhtajan between the Euphorbiales and Thymeleaceae, since the "crotonoid" or "stellate" sculpture pattern, with supratectal triangular and oblong projections arranged in a reticulum, is largely restricted to certain Thymeleaceae, Buxaceae, and Euphorbiaceae (Arkhangel'skiy, 1966a, 1966b). Again, this must be an example of parallelism, since other (presumably more primitive) members of both orders are reticulate and tricolporate; it is these that must be studied in more detail for indications of dilleniid versus rosid affinities.

Asteridae.—In keeping with their position as the most advanced subclass in the Takhtajan and Cronquist systems, the Asteridae show a broad spectrum of divergently specialized pollen types. Nevertheless, a few members of the putatively more primitive orders (Caprifoliaceae, *Adoxa*, Loasaceae, Hydrophyllaceae, Buddlejaceae) have relatively small, psilate to finely reticulate tricolporoidate pollen of the type considered above to be primitive in both the Dilleniidae and Rosidae. On the other hand, the tricolpate condition in some Labiatae, Scrophulariaceae, etc., like many other cases of small size (e.g., *Myosotis* in the Boraginaceae), is more easily explained in terms of the Takhtajan and Cronquist systems as a secondary specialization. In the case of the Labiatae, tricolporate pollen is found in the relatively primitive subfamily Ajugoideae and in the related but generally more primitive family Verbenaceae.

A more detailed survey would be required to determine whether the Asteridae are heterogeneous (as believed by Thorne, 1968). However, the "rosid" characters cited above are common enough to suggest that at least some of the Asteridae are rosid rather than dilleniid derivatives. The tendencies for oblate-triangular and sometimes syncolpate grains, which are most striking in the Myrtales, are also common in the Polemoniales (e.g., Boraginaceae, Lennoaceae, Hoplestigmataceae, and especially Hydrophyllaceae, some of which even have pseudocolpi alternating with the colporate apertures, as in Combretaceae), some Gentianales (Menyanthaceae), Lamiales (Verbenaceae), and Scrophulariales (Scrophulariaceae, Solanaceae, Acanthaceae). Striate sculpture may be seen in the Gentianaceae, Menyanthaceae, Polemoniaceae, and especially the Scrophulariales (Solanaceae, Nolanaceae, and Scrophulariaceae).

The Acanthaceae are one of the best examples of a family where the diversity of pollen morphological types was recognized as of systematic importance well before the modern "explosion" of palynological research (e.g., Lindau, 1895). Besides presumably primitive tricolporate grains, this family shows trends for multiplication and shortening of apertures, the origin of tri- and polyporate grains by "fading" in place (rather than shortening) of colpi (a trend also inferred in the Rubiaceae: cf. Erdtman, 1952), and diporate, syncolpate, and even spiraperturate grains.

A few of the more striking asterid specializations may be mentioned. Not only are polyrugate and polyforate grains common (e.g., Martyniaceae, Convolvulaceae, Plantaginaceae), but the trend to numerous equatorial apertures (polycolpate and polycolporate) is more widespread in the Asteridae than in other subclasses, especially in the Scrophulariales and Lamiales (apparently all Pedaliaceae, and many Scrophulariaceae, Bignoniaceae, Lentibulariaceae, Acanthaceae, Verbenaceae, and Labiatae), and also in Polemoniaceae, Rubiaceae, Campanulaceae, and Stylidiaceae. On the other hand, a few Gentianaceae (*Leiphaimos*) show what may be a unique return to the uniaperturate (monoporate) condition, apparently associated with reduction in size in a basically triporate group. The Apocynaceae and Asclepiadaceae have already been cited as showing a trend analogous to that in the Orchidaceae from single grains to tetrads and pollinia. Finally, just as in their inflorescence morphology, the Compositae show a new level of complexity in their exine structure,

with what is considered a second tectum developed within the first in all but the most primitive members, and the elaboration of echinate and (in the Liguliflorae) complex fenestrate sculpture patterns (cf. Wodehouse, 1935, and Skvarla & Turner, 1966, for discussions of the contributions of light and transmission electron microscopy, respectively, to phylogeny of the Compositae).

PALYNOLOGICAL TECHNIQUE

Pollen being the size it is, palynology is totally dependent upon use of various types of microscopes. Three major instruments (light, scanning electron, and transmission electron microscopes) are currently available for the study of pollen morphology.

The original and still basic method of studying pollen grains is with the light microscope (photomicroscopy). Palynological material is normally first subjected to an acid treatment or acetolysis (Erdtman, 1960) and then the acetolyzed pollen grains are mounted on permanent slides. Acetolysis performs two main functions: (1) it removes the pollen protoplast, a part of the pollen wall, viz., the intine, and material that may cover the pollen surface such as oil droplets and protein, i.e., pollenkitt and tryphine, and (2) it causes the outer pollen wall layer (exine) to turn from its normal light yellowish-green to a darker amber color. Both of these changes result in the production of greater pollen contrast and permit more detailed study of pollen grains than is possible with non-acetolyzed material. Walker (1971b, 1971d) has modified Erdtman's standard acetolysis method with two features in mind, namely, (1) introduction of a less drastic means of preparing pollen than boiling, which frequently causes a number of grains to be damaged, and (2) development of a method of acetolysis that can handle a large number of individual pollen samples rapidly. In this modified acetolysis treatment pollen is placed in corked centrifuge tubes with standard acetolysis fluid (9 parts acetic anhydride to 1 part concentrated sulfuric acid) in an oven overnight at 50–60°C. The material is then washed once with glacial acetic acid and three times with water. Acetolyzed pollen is then mounted in glycerine jelly and the slides ringed with an air-drying, phenolic varnish in order to make them permanent. The use of disposable Pasteur pipettes was found extremely helpful in transferring a mixture of pollen and glycerine jelly evenly to slides, especially when the available material is scanty. Taxa with reduced exine (such as Lauraceae, Musaceae, etc.) are subjected to KOH-treatment instead of acetolysis. Again, a corked centrifuge tube containing pollen material and varying concentrations of KOH (up to 1 N) is placed in an oven overnight at 50–60°C. The material is then washed in water 3–4 times, stained in basic fuchsin, toluidine blue, and/or alcian blue, and mounted in glycerine jelly.

Whole pollen mounts prepared by these techniques may be studied and photographed in the light microscope at the level of whole grain topography (to determine aperture type for example) and at highest magnification using various focal planes (i.e., LO-analysis) to analyze exine structure and sculpturing (cf. Erdtman, 1966). One may also photograph optical sections of the exine, especially as seen in median optical view. Thin-sections of the exine may also be prepared

for study in the light microscope using paraffin-embedded material and an ordinary rotary microtome (Tseng, 1971).

Pollen samples examined in the scanning electron microscope (SEM) should be subjected initially to acetolysis treatment (Hanks & Fairbrothers, 1970), then transferred from water to double adhesive tape and allowed to dry. Samples may be carbon-coated before coating with a heavy-metal such as gold-palladium prior to their placement within the microscope. The scanning electron microscope greatly complements light microscope studies. The main advantages of the SEM are: (1) great range of magnification, (2) relative ease with which specimens can be prepared for study, (3) considerable depth of focus, and (4) ability to show the pollen surface (sculptural elements) independent of underlying structural components. The last feature is especially important, since the SEM often aids in the interpretation of confusing or ambiguous LO-analyses seen in the light microscope (Walker, 1971d). Also, one may deliberately break pollen grains and study them with the SEM in order to acquire a three-dimensional view of the internal wall structure (cf. Cerceau-Larrival & Roland-Heydacker, 1972).

The transmission electron microscope (TEM) is vital for high resolution micrographs necessary for complete understanding of the pollen wall. The main advantage offered by the transmission electron microscope, besides higher magnification than the light microscope, is the ability to delimit and resolve ektexine-endexine and demonstrate the presence or absence of a foot-layer. Also, measurements of the different wall layers may be carried out much more accurately with transmission electronmicrographs in the case of small grains with thin exines. In some cases both cross and tangential sections are necessary to elucidate the nature of the pollen wall.

Major Palynological Reference Works

Mention must be made first of a number of journals which are devoted largely to papers concerned with comparative pollen morphology. The two leading journals in this area are *Grana* (formerly *Grana Palynologica*), which was started by Gunnar Erdtman, and *Pollen et Spores*, which is edited by M. Van Campo. Lately, a series of palynological monographs, the *World Pollen and Spore Flora*, edited by S. Nilsson, have appeared as supplements to *Grana*. A third journal which frequently contains systematic palynological papers, *Review of Palaeobotany and Palynology*, was started more recently. Other pollen journals include the *Journal of Palynology*, published in Lucknow, India, and the *Japanese Journal of Palynology* (published in Japanese).

Palynology is fortunate in having a number of excellent bibliographies, the most comprehensive being the biblographic supplement published by M. Van Campo each year in the journal *Pollen et Spores*. References published before Mme. Van Campo's bibliographic supplements were started may be found in the earlier palynological bibliographies published over many years by Gunnar Erdtman (cf. Erdtman, 1966, for references). Two other important pollen bibliographies have been published recently. The first of these, "Bibliography of Actuopalynology, 1671–1966," which was published in the journal *Review of Palaeobotany and Palynology*, Vol. 12(1–3), 1971, lists palynological papers by families, while

the second, "Bibliographic Index to the Pollen Morphology of Angiosperms" (Thanikaimoni, 1972), lists each reference by genus.

Books, articles, and reviews which are concerned largely with pollen terminology and/or comparative pollen morphology of angiosperms include publications by Erdtman (1943, 1952, 1963, 1964, 1966, 1969), Faegri & Iversen (1964), Felix (1961), Kapp (1969), Kremp (1965), Reitsma (1970a), Tschudy & Scott (1969), and Wodehouse (1935). Special mention must be made of Erdtman's (1952, 1966) monumental work, *Pollen Morphology and Plant Taxonomy. Angiosperms*, which summarizes what was known about the pollen morphology of every family of angiosperms up to about 1950.

Systematic palynological papers dealing with individual groups of flowering plants have been rapidly increasing every year. The following are just a few examples of angiosperm families which have been the subject of palynological studies since publication of Erdtman's book in 1952: Magnoliaceae (Canright, 1953; Agababian, 1972; Praglowski, 1974), Annonaceae (Walker, 1971b, 1971c, 1972b), Canellaceae (Wilson, 1964), Menispermaceae (Thanikaimoni, 1968), Phytolaccaceae (Nowicke, 1968), Gyrostemonaceae (Prijanto, 1970a), Bataceae (Prijanto, 1970b), Juglandaceae (Whitehead, 1965), Dilleniaceae (Dickison, 1967), Ochnaceae (Muller, 1969a), Sarcolaenaceae (Carlquist, 1964), Caryocaraceae (Barth, 1966), Bombacaceae (Fuchs, 1967), Flacourtiaceae (Keating, 1973), Passifloraceae (Presting, 1965), Fouquieriaceae (Henrickson, 1967, 1973), Droseraceae (Chanda, 1965), Leguminosae-Mimosoideae (Guinet, 1969; Sorsa, 1969), Haloragaceae (Praglowski, 1970b), Alangiaceae (Reitsma, 1970b), Icacinaceae (Dahl, 1952), Coriariaceae (Praglowski, 1970a), Euphorbiaceae (Punt, 1962; Köhler, 1965), Geraniaceae (Bortenschlager, 1967), Loganiaceae (Punt & Leenhouts, 1967), Gentianaceae (Nilsson, 1967), Menyanthaceae (Nilsson, 1973), Polemoniaceae (Stuchlik, 1967), Lennoaceae (Drugg, 1962), Compositae (Stix, 1960; Skvarla & Larson, 1965; Skvarla & Turner, 1966), Palmae (Thanikaimoni, 1970a; Sowunmi, 1972); Araceae (Thanikaimoni, 1969), Commelinaceae (Rowley, 1959), Rapateaceae (Carlquist, 1961), Centrolepidaceae (Chanda, 1966), Restionaceae (Chanda, 1966), and Flagellariaceae (Chanda, 1966).

SUMMARY AND CONCLUSIONS

Palynology, although a relatively recent branch of plant morphology, has already provided a great wealth of phylogenetically useful information, thanks both to the ease of extraction of great numbers of specimens and characters from minute amounts of herbarium material, and to the diversity of evolutionary trends, many of which can be verified directly from the fossil record. In angiosperms, the most important trends at the higher taxonomic levels involve the number, position, and structure of germination apertures (closely connected with the form and symmetry of the whole grain), exine structure and stratification, and in some cases size and sculpture.

With some exceptions, pollen morphology is consistent with the levels of relative advancement and the relationships postulated in the Takhtajan and Cronquist systems. Bilaterally symmetrical "gymnospermous" monosulcate pollen and derivative types (inaperturate, disulculate, etc.) characterize both the

putatively primitive dicotyledonous subclass Magnoliidae (sensu stricto) and the monocotyledons. Within the monocotyledons, the primitive monosulcate type is found in all four subclasses; the most striking specializations (monoporate grains, cryptotetrads, loss of exine, and pollinia) are seen in "higher" Commelinidae and Liliidae (grasses, sedges, Zingiberales, and Orchidales). The six non-magnoliid dicotyledonous subclasses are characterized by radially symmetrical tricolpate and derivative pollen types. Relatively primitive reticulate tricolpate pollen is retained by many Ranunculidae, "lower" Hamamelididae, and Caryophyllidae; the Ranunculidae and Caryophyllidae are united by a distinctive trend from tricolpate to globally symmetrical multiaperturate forms. The Dilleniidae (except Dilleniaceae) and Rosidae are somewhat more advanced in having basically compound-aperturate tricolporate pollen; both show parallel tendencies for increase in size and elaboration of exine structure, while the Rosidae show divergent trends related to oblate-triangular shape. The Asteridae exhibit the greatest array of specialized pollen types, but they retain indications of a rosid ancestry. The most important palynological contradiction of the Takhtajan and Cronquist systems is the fact that the highly specialized, basically triporate "higher" Hamamelididae (Amentiferae) can be more directly related to triangular tricolporate Rosidae than to the tricolpate "lower" Hamamelididae.

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THE BASES OF ANGIOSPERM PHYLOGENY: CYTOLOGY[1]

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ABSTRACT

A broad review of chromosome numbers in the angiosperms is presented according to the phylogenetic system of Cronquist. Consideration of the results indicates that the original basic chromosome number for the class as a whole, and for all but one of its subclasses, is or may well be $x = 7$. For Caryophyllidae, $x = 9$ is indicated. Families and taxa of higher rank can be compared only if the original basic chromosome number for the group is known, and there are many families where this is not the case. Evolutionary changes in chromosome number and morphology, particularly in herbaceous plants, have tended to give the impression that these characteristics were of limited utility in classification, and have often led to numerical coincidences between unrelated groups. In addition, many inaccurate counts have been reported, and vouchers, if present, are occasionally misidentified, giving rise to misleading conclusions. Electronic data processing should be applied to the field as soon as possible for efficient information retrieval, especially since the number of chromosome counts reported is growing annually. Well edited regional treatments, or those dealing with a particular taxonomic group, are encouraged. An initial burst of polyploidy is suggested for the angiosperms by the survival of many polyploid lines, especially among Magnoliidae and Hamamelididae. Although many families and even orders are of polyploid origin, progressive evolution in the group seems to have proceeded largely at the diploid level, and much of the major differentiation evidently occurred even among plants with the original basic chromosome number, $n = 7$.

For more than 50 years, chromosome cytology has been an important element in evaluating relationships and deducing phylogenetic sequences in the angiosperms. Data derived from this field are potentially useful, especially in woody plant groups (Darlington & Mather, 1949; Darlington, 1956), but the use of such data is not simple, as will be illustrated in the following pages. Changes in chromosome number and morphology may be rapid even within a genus (Stebbins, 1966), a tendency that had made many students of phylogeny mistrust or downgrade the importance of chromosomal information for broad considerations. Insufficient information, inaccurate information, and the necessity of understanding the pattern in one taxon before it can be compared on this basis with another taxon all contribute to the difficulty of using such information in systematic or evolutionary studies.

MATERIALS AND METHODS

The principal sources of information on the chromosome numbers of angiosperms are the compendia of Darlington & Janaki Ammal (1945), Darlington &

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Wylie (1955), and Bolkhovskikh et al. (1969). In addition, there is the annual *Index to Plant Chromosome Numbers*, the most recent number of which summarizes reports for 1972 (Moore, 1974). Some measure of the interest in chromosome cytology may be deduced from the fact that whereas counts for 1821 genera were summarized in 1945, there were 2693 by 1955 and 4679 by 1969 (including reports up to 1966). Electronic data processing could be applied very profitably to this field, and it ought in principle to be possible to add successive counts to a data bank which could be queried at any time for any taxon of interest. Editing is however a very serious problem; in the list of Bolkhovskikh et al. (1969) the same species are often listed under two or more generic names. With the changing limits of families, it is often no simple matter to know where to look for a given genus. Closely edited regional compendia such as that of Löve & Löve (1961) are likely to be most useful, but few people have the knowledge to edit a world chromosome list to this level. We shall probably see more and more regional treatments and treatments of particular taxa, such as families, in which the editing can reach a high standard.

A considerable and totally unnecessary element of confusion is introduced into all phylogenetic considerations by the fact that the *International Code of Botanical Nomenclature* limits the principle of priority to taxa of the rank of family and below. Thorne (1968, 1974) has used the principle of priority in determining the names of orders, while Cronquist (1968) and Takhtajan (1969) have not. There seems to be no advantage to anyone in arbitrarily using two or more names for the same order, and the simplest way to solve the problem, now that general agreement is becoming apparent on the limits of many orders, would be to apply the principle of priority to taxa at this rank also.

Even when the problems of information retrieval and editing of the data have been overcome, however, there remain a series of other difficulties. Reports of chromosome numbers prior to World War II were rarely associated with particular voucher specimens, and the identity of the plants cannot then be verified. Inaccurate counts are fairly frequent, especially in papers which contain listings for many families. All reports prior to 1920 were made from sectioned material, the interpretation of which presents special difficulties. In preparing the summary statements for various taxa in this paper, I have simply disregarded a number of counts which have not been verified or were included in papers suspected to contain a high proportion of erroneous counts.

It is of the utmost importance in the application of chromosomal information at the family level first to deduce the original basic chromosome number of the taxon in question. The bulk of this paper is devoted to a consideration of such hypotheses, since without knowing the original basic chromosome number of a family or other taxon, it is not possible directly to compare it with any other. Similar considerations have been pointed out by Thorne (1963), Cronquist (1968), and many others for deducing phylogenies in general; but numerical coincidence is so great that the matter becomes a particularly important one with respect to chromosome number.

RESULTS

GAPS IN THE RECORD

Of the 354 families recognized by Cronquist (1968), there are 44 for which no cytological information is available at present. They are listed with the number of genera and species and their ranges from Airy Shaw (1966):

Achariaceae (3/3, South Africa), Aextoxicaceae (1/1, Chile), Akaniaceae (1/1, eastern Australia), Alseuosmiaceae (3/11, New Caledonia, New Zealand), Ancistrocladaceae (1/20, Old World tropics), Balanopaceae (1/12, Australasia), Barbeyaceae (1/1, northeastern Africa, Arabia), Cardiopterygaceae (1/3, southeastern Asia, Australia), Caryocaraceae (2/25, tropical America), Cephalotaceae (1/1, Western Australia), Columelliaceae (1/4, South America), Corsiaceae (2/10, New Guinea, Chile), Dialypetalanthaceae (1/1, tropical America), Didymelaceae (1/2, Madagascar), Dipentodontaceae (1/1, temperate Asia), Ecdeiocoleaceae (1/1, Western Australia), Geissolomataceae (1/1, South Africa), Geosiridaceae (1/1, Madagascar), Grubbiaceae (2/3, South Africa), Hoplestigmataceae (1/2, tropical Africa), Hydnoraceae (2/18, South America, Africa), Julianiaceae (2/5, tropical America), Lissocarpaceae (1/2, tropical South America), Marcgraviaceae (5/100, tropical America), Mayacaceae (1/10, tropical America and Africa), Medusagynaceae (1/1, Seychelles), Medusandraceae (1/1, tropical Africa), Myrothamnaceae (1/2, Africa), Myzodendraceae (1/11, South America), Pentaphragmataceae (1/30, tropical Asia), Peridiscaceae (2/2, South America), Petrosaviaceae (1/3, tropical Asia), Picrodendraceae (1/3, West Indies), Quiinaceae (4/50, tropical South America), Rhoipteleaceae (1/1, southeastern Asia), Sarcolaenaceae (8/33, Madagascar), Siphonodontaceae (1/5, southeastern Asia, Australia), Stylobasiaceae (1/2, southwestern Australia), Thurniaceae (1/3, tropical South America), Tovariaceae (1/2, America), Tremandraceae (3/25 Australia), Trigoniaceae (4/35, tropical), Vochysiaceae (6/200, tropical America and Africa), and Xanthophyllaceae (1/60, tropical Asia).

Of the additional families recognized by Thorne (1968) and by Takhtajan (1969), there is no cytological information available for the following 49: Anisophylleaceae (4/36, tropical), Asteropeiaceae (1/7, Madagascar), Balanitaceae (1/25, Old World tropics), Biebersteiniaceae (1/5, Eurasia), Bonnetiaceae (3/22, tropical Asia and America), Bretschneideraceae (1/1, southwestern China), Brunelliaceae (1/45, tropical America), Diegodendraceae (1/1, Madagascar), Dirachmaceae (1/1, Socotra), Donatiaceae (1/2, subantarctic), Emblingiaceae (1/1, Australia), Eremosynaceae (1/1, Australia), Erythropalaceae (1/2, Indomalaysia), Goupiaceae (1/3, tropical South America), Halophytaceae (1/1, southern South America), Hanguanaceae (1/2, Ceylon, Malaysia), Hectorellaceae (1/1, New Zealand), Huaceae (1/2, tropical Africa), Hypseocharitaceae (1/8, Andes), Ixonanthaceae (8/48, tropical), Kirkiaceae (1/8, Africa), Koeberliniaceae (1/1, southern United States, Mexico), Lacistemataceae (2/27, tropical America), Lepidobotryaceae (1/1, tropical Africa), Lepuropetalaceae (1/1, America), Lophiraceae (1/2, tropical Africa), Octoknemaceae (1/6, Africa), Oncothecaceae (1/1, New Caledonia), Paracryphiaceae (1/2, New Caledonia),

Pelliceriaceae (1/1, tropical America), Pentadiplandraceae (1/2, Africa), Pentaphylacaceae (1/2, southeastern Asia), Phellinaceae (1/10, New Caledonia), Phyllonomaceae (1/8, tropical America), Plocospermataceae (1/3, Mexico, Central America), Podoaceae (2/3, southeastern Asia), Posidoniaceae (1/2, Mediterranean, Australia), Pterostemonaceae (1/2, Mexico), Roridulaceae (1/2, South Africa), Sargentodoxaceae (1/1, China), Schoepfiaceae (1/35, tropical), Strasburgeriaceae (1/1, New Caledonia), Surianaceae (1/1, tropical coasts), Tetracarpaeaceae (1/1, Tasmania), Tetrameristaceae (1/3, western Malaysia), Toricelliaceae (1/3, Himalayas, China), Trapellaceae (1/2, eastern Asia), Tribelaceae (1/1, temperate South America), and Vivianiaceae (1/30, South America).

It is hoped that the publication of these lists may help to promote the acquisition of cytological information about these families, as well as of such interesting additional groups as *Ctenolophon*, *Disanthus*, and *Piptocalyx*. Extreme care must be taken, however, to insure the accuracy of a few counts in a group made by themselves, as erroneous reports of chromosome number and chromosome morphology for an unknown group are much worse than no information at all.

In the course of preparing this summary statement, a number of families were reviewed for which the existing results indicated very interesting cytological patterns that would amply repay additional investigation. These families include: Acanthaceae, Bignoniaceae, Capparaceae, Combretaceae, Cyclanthaceae, Dilleniaceae, Gentianaceae, Malpighiaceae, Melastomataceae, Nyctaginaceae, Polygalaceae, Santalaceae, Sapindaceae, Sapotaceae, Sterculiaceae, and Verbenaceae. In general, it can be said that the plants of tropical America are very badly in need of cytological study. The extensive reports of S. and G. Mangenot from tropical Africa have shed much light on the plants of that continent, and have in fact included the only cytological reports of Rapateaceae and Humiriaceae, medium-sized and very interesting tropical American families each represented in Africa by a single species. In a similar way, the studies of J. B. Hair in New Zealand and of P. N. Mehra and his associates in the Himalayan region have been outstanding contributions. Other areas of great interest for additional work on chromosome numbers include South Africa, Madagascar, New Caledonia, Australia, and southern Asia.

Review of the Chromosome Numbers of Angiosperms

The following notes are based upon the sources mentioned above, and are arranged according to the system of Cronquist (1968). A persistent difficulty concerns the monophyletic nature of the group in question, whether it be an order, a family, a superorder, or a subclass. If it has been put together of discordant elements, the cytological deductions may be invalid. Nevertheless, it has appeared worthwhile to offer hypotheses, when possible, concerning the original basic chromosome numbers of various groups, and the role that chromosome information can play in evaluating their relationships.

TABLE 1. Basic chromosome numbers in Magnoliales.

1. Austrobaileyaceae	22[a]
2. Lactoridaceae	20 (or 21?)
3. Magnoliaceae	19
4. Winteraceae	13, 43
5. Degeneriaceae	12
6. Himantandraceae	12
7. Annonaceae	7 (Walker, 1972)
8. Myristicaceae	19, 21, 25
9. Canellaceae	14[b], 13
10. Illiciaceae	14, 13
11. Schisandraceae	14, 13
12. Eupomatiaceae	10
13. Amborellaceae	13
14. Trimeniaceae	8 (Goldblatt, 1974)
15. Monimiaceae, s. str.	19 (22, ca. 40, 43), 39
15a. Hortoniaceae (Smith, 1972)	19 (Goldblatt, 1974)
15b. Atherospermataceae	22 (21?)
15c. Siparunaceae	22
16. Gomortegaceae[c]	21 (Goldblatt, unpubl.)
17. Calycanthaceae	11
17a. Idiospermaceae	11 (Blake, 1972)
18. Lauraceae	12
19. Hernandiaceae	20
19a. Gyrocarpaceae	15

[a] Peter Goldblatt (1974) has reexamined mitosis in the cuttings from the plant on which Rüdenberg's (1967) report of $2n = 44$ was based. He found that the chromosomes were large, clearly differentiated, and unequivocally $2n = 44$ as reported. We suggest that the "pair of quite small submedian chromosomes" mentioned by Ehrendorfer et al. (1968: 342) may have been satellites, noted by Rüdenberg (1967).

[b] Goldblatt (1976a) has determined $2n = 28$ in *Canella alba* Murr. cultivated at the Missouri Botanical Garden.

[c] Plants grown in the University of California Botanical Garden, Berkeley, and previously reported as *Gomortega* (Raven et al., 1971), have been redetermined as *Beilschmeidia berteroana* (Gay) Kosterm., which therefore has $n = 12$ and $2n = 24$.

CLASS MAGNOLIOPSIDA (DICOTYLEDONEAE)

I. SUBCLASS MAGNOLIIDAE

I-1. *Magnoliales*.—The basic chromosome numbers in this order are summarized in Table 1. It now appears clear that $x = 7$ is the original basic chromosome number for this order and for the angiosperms (Raven & Kyhos, 1965; Stebbins, 1966; Ehrendorfer et al., 1968; Raven et al., 1971; Walker, 1972). As there is no evidence to support the present or past existence of plants with $n = 6$ or $n = 5$, it seems preferable to explain most of the tetraploid ($x = 12$, 13) numbers of these ancient families by aneuploid reduction from $n = 14$. Whether $n = 10$ in *Eupomatia* and $n = 11$ in *Idiospermum* and Calycanthaceae can be explained in the same way or by aneuploid increase from $n = 7$, as seems to have occurred in Annonaceae (Walker, 1972), remains to be seen. By an extension of this reasoning, Atherospermataceae, Austrobaileyaceae, Gomortegaceae, Hernandiaceae, Lactoridaceae, Magnoliaceae, Monimiaceae, Myristicaceae, and Siparunaceae are paleohexaploid; of these, Atherospermataceae, Siparunaceae, and Gomortegaceae could conceivably have had a common ancestor, whereas all of the other families seem to have been derived independently. The most frequent base number in Winteraceae, $n = 43$, which occurs in all genera except *Tasmannia* ($x = 13$), appears to be of paleododecaploid origin. Cytology provides no evidence for or against subdividing Magnoliales, as Thorne (1968) and Takhtajan (1969) have done.

I-2. *Piperales*.—Chloranthaceae consist of five genera; no chromosome counts are available for the monotypic *Ascarinopsis* of Madagascar. In *Hedyosmum*, $n = 8$ (two species). *Sarcandra* and *Chloranthus* have $x = 15$ (older counts of $2n = 28$ in *Chloranthus* should be confirmed), *Ascarina* (one count), $n = 14$. With the available information, the original basic chromosome number of the family

could be either $x = 7$ or $x = 8$. Saururaceae consist of four genera, with $x = 11$ in *Anemopsis* and *Saururus* and probably $x = 12$ in *Hottuynia* (several high and irregular numbers; apomixis). Piperaceae consist of four genera, including the vast genera *Piper* and *Peperomia*, which have been poorly sampled chromosomally. For *Peperomia*, $x = 11$ (Smith, 1966); the presence of other basic chromosome numbers should be reconfirmed. In *Piper* and *Pothomorphe*, no conclusion regarding basic chromosome number is possible at present, but $x = 12$, 13, and 14 are known; much more work will be necessary before the cytological situation in this genus is clarified. Cytological evidence supports the notion of a close relationship between Saururaceae and Piperaceae, but provides no indication of a relationship between Chloranthaceae and Piperaceae (Swamy, 1953; Smith, 1972). Chloranthaceae might better be placed in the Magnoliales as suggested by Thorne (1968) and Takhtajan (1969, Laurales), leaving the Piperales as a more homogeneous satellite order. This would appear to be supported by the conclusions of Hickey & Wolfe (this symposium).

I-3. *Aristolochiales*.—Aristolochiaceae consist of 7–10 genera, of which chromosome counts are available for three. In *Aristolochia*, there are many diploid species with $n = 7$, and some aneuploid (to $n = 4$) and polyploid derivatives. In *Asarum*, $x = 13$ (in *Asarum* and *Hexastylis*) and 12 (in *Heterotropa*). In the Indo-Malaysian shrubby *Apama*, $n = 13$ is the only available chromosome count. It is reasonable to assume that the basic number for the family and order is $x = 7$, with aneuploid reduction at either the diploid or tetraploid level to produce $x = 13$. Aristolochiaceae have often been considered directly related to Annonaceae, and both have $x = 7$.

I-4. *Nymphaeales*.—Nymphaeaceae consist of *Nymphaea*, $x = 14$; *Nuphar*, $x = 17$; *Euryale*, $n = 29$; and *Victoria*, perhaps $x = 12$. The cytological relationships confirm the morphological and anatomical evidence of a number of very distinct, loosely related genera. *Barclaya*, sometimes segregated as a distinct family (Takhtajan, 1969), has $n = 18$ and possibly $n = 17$. In the group often recognized as Cabombaceae (Takhtajan, 1969; Thorne in Becker, 1973), *Cabomba*, based on several rather old counts, has $n = 12$ and $n = 52$ in the same species and *Brasenia* has $n = 40$. In Nelumbonaceae, the only genus, *Nelumbo*, has $n = 8$, a very distinctive chromosome number even within this heterogeneous group. Taken at face value, this tends to support Takhtajan's (1969) segregation of this family as a distinct order (see also Smith, 1972). Finally, in Ceratophyllaceae, the basic chromosome number of the only genus, *Ceratophyllum*, might be $n = 12$, but the evidence, based on scattered, diverse, and rather old chromosome counts, is insufficient. A detailed chromosomal analysis of Nymphaeales, taking into account chromosome morphology as well as number, appears a promising subject for investigation, even though at least one count is available for all but one of the recognized genera in the order. If *Nelumbo* is excluded, the order may have had a polyploid original basic number.

I-5. *Ranunculales*.—In general, this order is characterized by relatively low chromosome numbers and large chromosomes. In Ranunculaceae, $x = 7$, 8, 9. Podophyllaceae, added to Ranunculaceae by Cronquist (1968), have $x = 6$ in four of the six genera, $n = 7$ in the monotypic, Japanese *Ranzania*. Chromosomally

as well as morphologically they could be regarded as intermediate between Berberidaceae, where they have usually been placed, and Ranunculaceae (Airy Shaw, 1966). In Berberidaceae, $x = 6$ and, in *Berberis* (*Mahonia*), $x = 14$. The Leonticaceae, segregated by Airy Shaw (1966) from Berberidaceae, have $x = 6$ and 8 (7, 9). *Nandina*, considered very distinct in Berberidaceae, is likewise distinct cytologically, with $n = 10$, a unique chromosome number in the order. This would in itself tend to support Takhtajan's (1969) treatment of Nandinaceae as a separate family. The only species of *Circaeaster* (Circaeasteraceae) has $n = 15$. The subfamily Hydrastoideae of Ranunculaceae is very distinct cytologically, with $n = 10$ in *Glaucidium*, $n = 13$ in *Hydrastis*, and this seems to be in accordance with its segregation as a distinct family or families by Airy Shaw (1966) and Takhtajan (1969).

Lardizabalaceae, with $x = 16$, 15, and 14 (see also Ratter & Milne, 1973), and Menispermaceae, with $x = 13$ and 12, have large chromosomes also and chromosome numbers that are clearly secondarily derived within this order. Sabiaceae are also included by Cronquist (1968) here, and *Meliosma*, with $x = 8$, is compatible with the other families of the order on cytological grounds. The segregation of Meliosmaceae from Sabiaceae as a distinct and possibly not closely related family by Airy Shaw (1966) receives support from the only known chromosome number in *Sabia*, $n = 12$. Both Sabiaceae and Meliosmaceae would fit equally well on cytological grounds in Sapindales (Takhtajan, 1969) or Rutales (Thorne, 1968). On chromosomal grounds, Coriariaceae, with $x = 20$ and small chromosomes fit very poorly in this order, as do Corynocarpaceae, with $n = 22$. Coriariaceae appear to fit better in Rosales (Thorne, 1968) or Rutales (Takhtajan, 1969) on the basis of cytology, whereas Corynocarpaceae fit better in Celastrales (Takhtajan, 1969) or Rosales (Thorne, 1968). On the other hand, Papaveraceae, included in the order by Thorne (1968), appear to fit well in the Papaverales (see order I-6).

I-6. *Papaverales*.—Of the three subfamilies of Fumariaceae (Ernst, 1962), $x = 8$ in the unigeneric Hypecoideae and (with various aneuploid derivatives) in the Fumarioideae also. In the monotypic Japanese (and probably relictual) Pteridophylloideae, $n = 9$. In the Papaveraceae, $x = 7$ is common, with $x = 6$ a frequent aneuploid derivative; but among the more primitive, perennial members of the Chelidonioideae (Ernst, 1962), $x = 10$ in *Stylophorum*, *Bocconia*, and *Macleaya* and $x = 9$ in the closely related *Sanguinaria* and *Eomecon*. What is probably a relatively unspecialized member of Papaveroideae, *Romneya*, has $n = 19$. Considering that Fumariaceae are on morphological grounds clearly derived from Papavaraceae, and taking into account the distribution of these chromosome numbers, $n = 10$ appears to be the original basic chromosome number for the order, and for Papaveraceae, and $n = 9$ the original basic chromosome number for Fumariaceae.

II. SUBCLASS HAMAMELIDIDAE

II-1. *Trochodendrales*.—The only species of Tetracentraceae has $n = 24$ (possibly 23, Ratter & Milne, 1973; Ratter, personal communication) and not $n = 19$ as reported earlier by Whitaker (1933). The only species of Trochodendra-

ceae, on the other hand, has $n = 20$ (Ratter & Milne, 1973) and not $n = 19$ as reported by Whitaker (1933). As pointed out by Ratter & Milne (1973), cytological evidence could be used to support Hutchinson's (1959) association of *Euptelea* ($n = 14$) with *Trochodendron*, if the genera are respectively tetraploid and hexaploid on $x = 7$.

II-2. *Hamamelidales.*—Among the smaller families of this order, Cercidiphyllaceae have $n = 19$, Eupteleaceae $n = 14$, Platanaceae $n = 21$ (with a series of other dubious reports), and Myrothamnaceae and Didymelaceae are unknown. In the central family, Hamamelidaceae, both the very distinct *Liquidambar* and the genus *Altingia*, sometimes segregated with it as a separate family, Altingiaceae, have $n = 16$ (Santamour, 1972; P. Goldblatt, unpublished). The only count available for the Exbucklandioideae, $n = 32$ in *Exbucklandia populnea* (R. Br. ex Griff.) R. W. Brown [as *Symingtonia populnea* (R. Br. ex Griff.) van Steenis; Mehra & Khosla, 1972], is in agreement with a base chromosome number of $x = 16$. In contrast, the Hamamelidoideae, based on abundant determinations of chromosome number, uniformly have $x = 12$ (8 genera), *Rhodoleia teysmannii* Miq., the only species of Rhodoleioideae for which chromosomal information is available, likewise has $n = 12$ (Goldblatt, unpublished). Counts for the monotypic Disanthoideae would be welcome. The chromosomal evidence indicates a fundamental gap between the Hamamelidoideae and Rhodoleioideae on the one hand and the Liquidambaroideae (with *Altingia*) and Exbucklandioideae on the other.

II-3. *Eucommiales.*—The only species has $n = 17$.

II-4. *Urticales.*—Ulmaceae may have had original basic chromosome numbers of $x = 14$ and $x = 10$, the former in *Ulmus*, *Zelkova*, and probably *Holoptelea* and the latter in *Celtis* (other reports need to be confirmed), *Chaetachme*, and *Trema*. How these two chromosome numbers relate is unknown, and more records for the family would be highly desirable. Moraceae probably also had $x = 14$, with $x = 13$ a frequent derivative. Aneuploidy is common in *Dorstenia*. Cannabaceae have $n = 10$ in both genera, although lower numbers have also been reported in *Humulus*. On cytological grounds, they do not appear closely related to Moraceae, and may represent the end product of another evolutionary line; their segregation at a family level appears warranted. In Urticaceae, $x = 14$, 13 and 12 are all well represented, with $x = 11$, 10, 8, and 7 found in some genera. *Parietaria* has $n = 7$, 8, 10, and 13, and the only species of *Pellonia* counted to date has $n = 8$; both genera would doubtless be rewarding subjects for further cytological investigation. For the order Urticales and the families Ulmaceae, Moraceae, and Urticaceae, an original basic chromosome number of $n = 14$, itself tetraploid, seems clearly to be indicated, with subsequent aneuploid reduction in Urticaceae and in the evolution of Cannabaceae. The presence of both $x = 10$ and $x = 14$ in Ulmaceae is the least understood cytological feature of the order. The monotypic Barbeyaceae are unknown cytologically, but recognized as a distinct order by Takhtajan (1969).

II-5. *Leitneriales.*—The single species has $n = 16$, as does Juglandales.

II-6. *Juglandales.*—Juglandaceae have $x = 16$. The West Indian Picrodendraceae, placed by Thorne (1968) in Euphorbiaceae and by Airy Shaw (1966) near

that family, are unknown cytologically, as are Rhoipteleaceae, consisting of a single species of tropical Asia with a wood structure similar to that of Aceraceae.

II-7. *Myricales*.—The only family, Myricaceae, has $x = 16$, as does Juglandales. Perhaps the preceding three orders are better placed in Rutiflorae where they would be morphologically and anatomically better matched (Thorne, 1968). Cytologically the matter is not clear.

II-8. *Fagales*.—Fagaceae have $x = 12$ (scattered records of $x = 11$ and $x = 10$ require confirmation), except for *Nothofagus*, with $n = 13$. The ditypic and presumably relictual *Trigonobalanus* has $n = 22$ (Soepadmo, 1972). Recently, $2n = 28$, together with $2n = 26$, 30, and 32 has been reported for *Quercus castaneifolia* C. A. Meyer (Tutajuk & Turchaninova, 1970), but these numbers were said to occur together in the same tissues, as did $2n = 24$, probably the actual chromosome number in this species as in other oaks. Betulaceae have $x = 14$ in *Alnus*, *Betula*, and *Corylus*, and $x = 8$ in *Carpinus*, *Ostrya*, and *Ostryopsis* (Carpinaceae), which are therefore a very distinct group within the order cytologically. The original basic chromosome number for the order may have been $n = 7$, with early polyploidy. Balanopaceae, very doubtfully related to Fagales (R. F. Thorne, personal communication), are unknown cytologically.

II-9. *Casuarinales*.—The original basic chromosome number in *Casuarina*, the only genus, is very probably $x = 9$, with a considerable number of aneuploid changes in the course of evolution (Barlow, 1959; Smith-White, 1959). In subg. *Gymnostoma*, the more primitive of the two subgenera, $n = 8$ in the only species counted. On cytological grounds, Casuarinales fit reasonably within Cronquist's (1968) subclass Hamamelididae; most morphological similarities may be attributable to convergent evolution for anemophily.

III. SUBCLASS CARYOPHYLLIDAE

III-1. *Caryophyllales*.—Phytolaccaceae, although poorly sampled, have an original basic chromosome number of $x = 9$, and all taxa examined, including *Petiveria*, have some multiple of that number. Gyrostemonaceae, regarded as a distinct family by Thorne (1968) and Takhtajan (1969), have $n = 14$–15 (P. Goldblatt, unpublished) and are certainly not related to the other families of Caryophyllidae. No information is available for the recently recognized Halophytaceae and Hectorellaceae. Cactaceae have $x = 11$, with relatively little aneuploidy or polyploidy. Aizoaceae (and Tetragoniaceae; Takhtajan, 1969) have $x = 9$, with a few aneuploid changes, especially to $x = 8$. Molluginaceae also have $x = 9$. Basellaceae probably have $x = 12$, with $x = 11$ in *Basella rubra* L. Chenopodiaceae have $x = 9$, with very little aneuploidy but frequent polyploidy. Amaranthaceae and Portulacaceae have some genera with $x = 9$, but such abundant aneuploidy that it would not be possible without detailed study of the respective families to ascertain the original basic chromosome numbers. Nyctaginaceae, although they are cytologically difficult, display such an array of chromosome numbers among the relatively few taxa that have been counted that it would clearly be of great interest to know more. The two species of Didiereaceae that have been examined cytologically had $2n =$ ca. 150 and $2n =$ ca. 190–200, respectively.

In Caryophyllaceae, subfamily Paronychioideae have $x = 9$, 10 and 8; subfamily Alsinoideae, $x =$ 10, 11, 12, 13, with $x = 9$ in *Cerastium* and $x = 14$ in *Myosoton*; and subfamily Silenoideae, $x = 12$, with $x = 10$ in *Vaccaria* and *Drypis*. Some species of *Paronychia* and the monotypic *Chaetonychia* have $n = 7$, evidently as a result of descending aneuploidy.

Considering that Phytolaccaceae are, in many respects, the most generalized family of the order, and considering the distribution of chromosome numbers among the other families, it appears likely that $x = 9$ is the original basic chromosome number for Caryophyllales.

III-2. *Batales.*—*Batis*, the only genus, has $n = 9$, a number compatible with Caryophyllales.

III-3. *Polygonales.*—Frequent basic chromosome numbers in the Polygonaceae, the only family, are $x = 10$, 11, and 12, with $x = 7$, 8, and 9 represented in the tribe Rumiceae, $x = 9$ in *Calligonum*, and $x = 9$ in two species of *Eriogonum*. Chromosome numbers below $n = 10$ in Polygonaceae seem clearly to have been derived by aneuploid reduction.

III-4. *Plumbaginales.*—In Plumbaginaceae, the only family, $x = 7$ in Plumbagineae without much doubt, with $x = 8$ possibly the original basic chromosome number in Staticeae (H. G. Baker, personal communication), judging by its occurrence in the relatively unspecialized *Gomiolimon* and *Acantholimon*, as well as (together with $n = 9$, 7, and 6) in *Limonium*. Since Plumbagineae are manifestly not as specialized as Staticeae, $x = 7$ may cautiously be advanced as the original basic chromosome number for the family, as suggested by H. G. Baker (personal communication). Cytological evidence does not therefore support the placement of this family in Caryophyllidae.

IV. SUBCLASS DILLENIIDAE

IV-1. *Dilleniales.*—Very few chromosome counts are available for the phylogenetically critical Dilleniaceae. It may be that $x = 8$ in *Dillenia* and *Hibbertia*; the only count available for *Tetracera* is $n = 12$, and the only one for *Wormia* is $n = 13$. For *Curatella americana* L., $n = 13$ and ca. 12 have been reported. It would be of very great interest to obtain more information. Paeoniaceae, $x = 5$, and Crossomataceae, $x = 12$, are very distinct from one another cytologically (Raven & Cave, 1963).

IV-2. *Theales.*—For Ochnaceae, $x = 12$ in two genera, 14 in two others (*Ouratea* has predominantly $x = 14$; one species has $n = 13$, Bawa, 1973), and $x = 19$ in *Sauvagesia*. The latter number, coupled with reports of $2n = 35$ in *Ochna serrulata* Walp., strongly suggests an original basic chromosome number for the family of $x = 7$, with aneuploid decrease from $n = 14$ to $n = 12$. Strasburgeriaceae, recognized as a distinct family by Thorne (1968) and Takhtajan (1969), are unknown cytologically, as are Marcgraviaceae, Caryocaraceae, Quiinaceae, Medusagynaceae, Sarcolaenaceae and Sphaerosepalaceae (Rhopalocarpaceae), the latter placed by Thorne (1968) in the order Malvales; Dipterocarpaceae have $x = 7$, 6, 11, and 10. In Theaceae, $x = 21$ in the related genera *Adinandra* and *Eurya*, with $n = 22$ and $n = 23$ in other species of *Eurya*; x apparently $= 10$ in *Ternstroemia*; $x = 15$ in several genera; and $x = 18$ in the monotypic *Franklinia*,

which is closely related to *Gordonia* and *Stewartia* with $x = 15$, a number also found in the Asian *Schima*. It might be that $x = 7$ is the original basic chromosome number for the family, with increasing aneuploidy and subsequent polyploidy; but many more chromosome counts will be necessary before this can be determined with any degree of certainty. The monogeneric Stachyuraceae have $n = 12$. In Actinidiaceae, *Saurauia* has $n = 30$ and *Actinidia* a series of high chromosome numbers of which $n = 29$ is the lowest reported. Clusiaceae (Guttiferae) appear to have $x = 7$, 8, 10 and perhaps 9 as important basic numbers (Robson & Adams, 1968). For *Hypericum*, Robson and Adams suggest $n = 12$ as the original basic chromosome number, with descending aneuploidy to $n = 7$. More chromosomal information is required for a clear understanding of evolution in this family. For Elatinaceae, scattered counts indicate $x = 9$, 10, and 12.

No definite conclusion can be drawn as to a possible original basic chromosome number for Theales, but $x = 7$ is an important number, with ascending aneuploidy evidently frequent.

IV-3. *Malvales*.—For Elaeocarpaceae, $n = 14$ in *Aristoelia* and *Muntingia*. There is one count each of $n = 12$ and $n = 15$ in *Elaeocarpus*, and *Sloanea* has $n = 13$. The two chromosome counts available for Scytopetalaceae, each from a different genus, are $n = 11$ and $n = 18$. In Tiliaceae, $x = 9$ and 8 are important basic chromosome numbers, with $x = 10$ in Brownlowioideae and $x = 7$ in *Corchorus*. In the cytologically very interesting Sterculiaceae, $x = 10$ is a recurrent basic chromosome number in several groups; numbers are reduced to $n = 6$ in two genera of Hermannieae; and basic numbers of $x = 18$, 20 and 21 occur in Sterculieae. The original basic chromosome number might be $x = 10$. Bombacaceae have high chromosome numbers and are difficult cytologically: $n = 36$ is most frequent with $n = 72$ (Baker & Baker, 1968), but other numbers such as $n = 43$, 44, 45, 46, and 48 (e.g., Bawa, 1973) also occur. Counts of $n = 14$ and 28 have been reported for *Durio zibethinus* L., but are badly in need of confirmation. Malvaceae, well sampled but very complex cytologically, seem to have $x = 7$ in the tribes Malveae (Bates & Blanchard, 1970; D. M. Bates, personal communication) and Ureneae, $x = 13$ in Gossypieae, and a variety of mostly higher numbers in Hibisceae. For Malvales as a whole, $x = 7$ is an important basic chromosome number, but $x = 10$ appears likely at present for Sterculiaceae and Tiliaceae, perhaps as an ancient reduction from $n = 14$. The same might be true for a hypothetical $x = 12$ (H. G. Baker, personal communication) in Bombacaceae. In Malvaceae, $x = 7$ is probably the original basic chromosome number, as suggested by Krapovickas (1972).

IV-4. *Lecythidales*.—For Lecythidaceae, sensu stricto, a tropical American group, one count of $n = 17$ has been obtained for *Bertholletia*, one of $n = 18$ for *Couroupita*; there are some 15 genera. For the Old World tropical family Barringtoniaceae, not recognized by Cronquist (1968), $x = 13$ in three of five genera. *Napoleona*, one of the two genera of Napoleonaceae, has two species counted with $n = 16$. No counts are available for the monotypic Brazilian *Asteranthos*, also segregated by some students as a distinct family. Cytological evidence is not in agreement with Takhtajan's (1969) placing Lecythidaceae

sensu lato, in Myrtales; the known pattern is more compatible with a position in Dilleniales (Theales; Thorne, 1968), or near that order (Cronquist, 1968).

IV-5. *Sarraceniales.*—In Sarraceniaceae, $n = 13$ in all species of *Sarracenia* that have been examined cytologically, $n = 15$ in the monotypic *Darlingtonia*, and $n = 21$ in the monotypic *Heliamphora*. *Nepenthes*, only genus of Nepenthaceae, had $n = 39$ in the two species that have been reported. In Droseraceae, *Dionaea* has $n = 16$; *Drosophyllum* $n = 6$; *Allovandra* $n = 19$ (24?); and *Drosera* $x = 10$ in most species, but $n = 13$, 14, 16, 17, and 23 have also been reported, the last two counts both in *D. binata* Labill. In the system of Thorne (1968) these families are widely separated, but Cronquist (1968) does not argue for a close relationship either; cytology certainly provides no indication of a close relationship between them.

IV-6. *Violales.*—In Flacourtiaceae, with some 93 genera and 1000 species, representatives of 12 genera and 19 species have been reported, with basic chromosome numbers of $x = 12$ and 11 most frequent. The only count for *Oncoba* was $n = 10$. Two species of *Flacourtia* had $n = 11$, one, $n = 9$. The bigeneric Lacistemaceae have not been examined cytologically, nor have Achariaceae, Ancistrocladaceae, Hoplestigmataceae, or Peridiscaceae. The only reported count for Dioncophyllaceae was $n = 18$. The monotypic Scyphostegiaceae have $n = 9$ (Ding Hou, 1972). Violaceae have *Rinorea* with $x = 12$, *Decorsella* with $n = 10$, *Hymenanthera* and *Melicytus* with $x = 16$ (based on $x = 8$?), *Hybanthus* with $x = 6$ and 4 (Bennett, 1972); and *Viola* perhaps with $x = 12$ but aneuploidy down to $n = 5$ and up to $n = 13$ (or 17). Turneraceae, on the basis of few counts, have $x = 5$ in *Turnera* (R. Ornduff, personal communication) and $n = 7$ in *Piriqueta*. Passifloraceae have $x = 12$ in two genera, $n = 11$ in two others, and $x = 9$ in *Passiflora* (two species with $n = 6$ doubtlessly derived). Malesherbiaceae, with a single genus, have $x = 7$. Bixaceae have $n = 7$ and $n = 8$ both reported in *Bixa*, which ought to be examined further, and $n = 6$ in *Cochlospermum*, the large chromosomes and low numbers of these two genera being in accordance with Cronquist's merging of Cochlospermaceae with Bixaceae. In Cistaceae, $x = 12$ in *Tuberaria*, with $n = 7$ in one species; $x = 12$, 11, 10 (commonest number), 9, and 5 in *Helianthemum*; $x = 9$ in *Cistus* and *Halimum*; and $x = 16$ (probably $x = 8$) in *Fumana*. All species of Tamaricaceae that have been counted have $n = 12$. On the basis of five species of *Frankenia* counted, Frankeniaceae seem to have $x = 5$. Fouquieriaceae have $x = 12$, thus agreeing with Tamaricaceae, but also with Solanales where they are placed by Thorne (1968). Caricaceae have $x = 9$ in *Carica*, the only genus for which counts are available. Loasaceae may have $x = 7$ (H. J. Thompson, personal communication), with $x = 14$ in *Loasa* and *Mentzelia*, $n = 13$ in *Cevallia*, n = 21 in all species of *Eucnide*, $n = 12$ in *Blumenbachia*, $n = 8$ and 7 in *Caiophora*, and $n = 37$ in *Gronovia*. Cytologically the family would fit equally well in Polemoniales, where it is placed by Takhtajan (1969). In *Begonia*, the only genus of the family that has been examined cytologically, all gametic chromosome numbers from $n = 8$ to 18, as well as many higher numbers, have been reported. The number $n = 14$ is most frequent, and R. A. H. Legro (personal communication) has suggested a hypothetical original basic chromosome number for the family of $x = 7$. Datiscaceae have *Datisca* with $n = 11$ and

Tetrameles with $n =$ ca. 23. Cucurbitaceae (Jeffrey, 1962) commonly have basic chromosome numbers of $x = 12$ and 11, less commonly $x = 13$, 14, 10, 9, and 8. Cytologically, they are very similar to the closely related Passifloraceae. *Mormordica*, of the tribe Joliffieae, has both $n = 14$ and $n = 11$; in Cucurbiteae, *Luffa* has $n = 13$ and $n = 11$; and in Melothrieae, the monotypic South American *Cucurbitella* has $n = 13$. *Seyrigia* (Madagascar), the only genus of the mostly tropical American Anguriinae for which cytological information is available, has $n = 13$ also. Cyclanthereae have $x = 8$. Considering the distribution of these counts, $x = 13$ or even $x = 14$ may be suggested as the original basic chromosome number of the family. For the order, $x = 7$, with early tetraploidy and aneuploid reduction preceding the origin of several families, seems likely at present.

IV-7. *Salicales*.—All three genera have $x = 19$.

IV-8. *Capparales*.—For Capparaceae, which are interesting cytologically but have been relatively poorly sampled, $x = 10$ or 11 might be a likely original basic chromosome number, judging from its representation in subfamilies Capparoideae and Cleomoideae. If that proves to be the case, there has been descending aneuploidy in both lines and then the formation of the secondary polyploid number $x = 17$ in *Cleomella* and some species of *Cleome*. In Brassicaceae, *Stanleya*, *Pringlea*, and *Ornithocarpa* (Rollins, 1969), three of the least specialized genera, have $x = 12$, as do *Draba* (with descending aneuploidy to $x = 8$; G. A. Mulligan, personal communication), *Selenia*, *Orychophragmus*, *Brasicella*, *Kremeria*, *Aethionema*, *Rhynchosinapis*, and some species of *Thlaspi* (also $x = 7$), *Sinapis* (also $x = 9, 7$), *Lobularia* (also $x = 11$), *Iberis* (also $x = 11, 10, 9, 7$), *Ionopsidium* (also $x = 11, 8$), and *Brassica* (also $x = 11, 10, 9, 8$). Genera in which $x = 11$ are *Xerodraba*, *Parolinia*, *Menonvillea*, *Morettia*, *Notoceras*, and *Eruca*, as well as some species of *Leavenworthia*, *Nerisyrenia*, *Diplotaxis*, *Smelowskia* ($n = 6$ also reported), *Ionopsidium*, *Iberis*, and *Heliophila*. Although the base number $x = 7$ is frequent in this family, $x = 6$ is very scattered and occurs either in obviously specialized genera or in descending aneuploid species within genera. The lowest chromosome numbers in the family occur in the Australian *Stenopetalum* and the American *Physaria*, $x = 4$ (also $x = 5$ in both, and $x = 6$ in *Stenopetalum*). At this time, $x = 12$ appears a reasonable choice for the original basic chromosome number of Brassicaceae, even though $x = 13$ and 14 are found in such primitive genera as *Streptanthus*, *Thelypodium*, and *Caulanthus*, and $x = 14(7)$ might ultimately prove to be correct. In Resedaceae, $x = 10$ occurs in three of the four genera for which chromosome information is available, with $x = 6$ also present in *Reseda*. For *Oligomeris*, counts of $n = 14$ and $n = 24$ have been reported for the only species examined. The three species of *Moringa*, only genus of Moringaceae, which have been examined cytologically all had $n = 14$. For the original basic chromosome number of the order, $x = 12$, 11, or 10 appear the most likely candidates on the basis of information currently available. No counts are available for Tovariaceae.

IV-9. *Ericales*.—Cyrillaceae have $x = 10$, Clethraceae $x = 8$. In Ericaceae, $x = 12$, found in all four subfamilies, may be the original basic chromosome number, with $x = 13$ and 11 frequent aneuploid derivatives, and $x = 7$, 8, and 16

found in one genus each. The cytologically very diverse Epacridaceae seem to have $x = 6$ (Smith-White, 1959), which suggests that the closely related Ericaceae may have had a tetraploid origin. Empetraceae have $x = 13$. In Pyrolaceae two genera probably have $x = 13$, one $n = 19$, and *Pyrola* $x = 23$ ($n = 12$ also reported, possibly reliably). Monotropaceae have $x = 8$, 13, 14, and possibly $x = 11$. In the evolution of Ericales, $x = 6$ was probably the original basic chromosome number, with $x = 12$ being present in the common ancestor of Ericaceae, Pyrolaceae, and Monotropaceae, but $x = 13$ possibly in the common ancestor of the last two families, as in the ancestor of Empetraceae. On cytological grounds, Cyrillaceae and Clethraceae seem to fit poorly in this order, and have chromosome numbers that accord better with those in Theales, where they are placed by Thorne (1968).

IV-10. *Diapensiales.*—The only family, Diapensiaceae, has $x = 6$, as postulated for Ericales. This seems to support its placement here rather than in Rosales as suggested by Thorne (1968).

IV-11. *Ebenales.*—Sapotaceae have $x = 12$ in 10 of the genera for which counts are available, $x = 13$ in five, $x = 11$ in two, and $x = 10$ in one, and $n = 13$ and $n = 22$ are both reported for *Sideroxylon.* Ebenaceae, certainly closely related to Sapotaceae, have $n = 15$ (F. White, personal communication), with $n = 12$ reported once (Gadella, 1972). Styracaceae have $n = 8$ in *Styrax*, $n = 12$ in *Pterostyrax* and *Halesia.* For Symplocaceae, $x = 11$ has been reported for seven Asian species of *Symplocos*, $n = 12$ for one from Puerto Rico. For Ebenales, only a very tentative suggestion of $x = 12$ as the original basic chromosome number can be made. No counts are available for Lissocarpaceae.

IV-12. *Primulales.*—Theophrastaceae have $x = 18$ in *Jacquinia* and *Clavija* ($n = 20$ also reported), and $n = 13$ in one report of *Deherainia.* Myrsinaceae have $x = 12$ and $x = 10$, with several genera, including *Aegiceras* ($x = 23$), polyploid. Judging from its distribution and relationship with $x = 23$, $x = 12$ is almost certainly the original basic chromosome number. Primulaceae might have $x = 12$, with $x = 12$, 11, 10, 8, 15, and 28 in the tribe Lysimachieae; $x = 12$, 11, 10, 14, 15, and 17 in Cyclamineae; $x = 12$, 11, 10, and (in *Primula*) 9 and 8, as well as secondarily polyploid numbers in Primuleae; and $x = 12$, 13, and 18 in *Samolus*, only genus of Samoleae. The monotypic *Coris*, sometimes segregated as a distinct family, has $n = 9$, which is certainly distinctive in Primulaceae. It is possible that $x = 12$ for Primulales.

V. SUBCLASS ROSIDAE

V-1. *Rosales.*—One species of Eucryphiaceae has $n = 15$ (P. Goldblatt, unpublished). Cunoniaceae have $n = 12$ in *Pancheria*, $n = 16$ in four genera, including *Cunonia*, and $n = 15$ in its relative, *Weinmannia.* More counts are highly desirable. *Bauera*, sometimes segregated as a distinct family, has $n = 16$. The monotypic Davidsoniaceae have $n = 16$ also (B. G. Briggs, personal communication). No counts are available for *Brunellia.* Pittosporaceae have $n = 12$ in *Pittosporum* and *Sollya* and $n = 18$ in *Citriobatus.* For Byblidaceae, $n = 7$ and $n = 12$ are reported for the two species of *Byblis*, respectively. For Hydrangeaceae, $x = 13$ is a frequent basic number, with $x = 11$, 10, 14, 18, 17, and 16 also

represented. *Carpentaria*, a monotypic genus of California with $n = 10$, might be related to an early aneuploid reduction. The original basic number for the family might be $x = 7$. For the elements of Cronquist's (1968) very inclusive Grossulariaceae, the following results are available—Brexiaceae: *Ixerba*, $n = 25$; *Brexia*, $n = 32$. Escalloniaceae: *Escallonia*, $n = 12$; *Carpodetus*, $n = 15$ (14?). Iteaceae: *Itea*, $n = 11$. Montiniaceae: *Montinia*, $n = 34$ (Goldblatt, 1976a). Grossulariaceae, sensu stricto: *Ribes*, $n = 8$. Polyosmeae, $n = 16$. In Bruniaceae, the unspecialized genus *Audouinia* has $n = 11$; other genera are evidently palaeopolyploid with $x = 22$ in *Staavia*, *Lonchostoma* and *Raspalia*, probably $x = 23$ in *Brunia* and *Nebelia*, while the most advanced genus, *Berzelia*, has $x = 20$ (Goldblatt, 1976b).

Cronquist's Saxifragaceae includes groups segregated as follows—Francoaceae, $x = 13$ (one count). Parnassiaceae, $x = 9$ (8?). Penthoraceae, $x = 8$, 9. Vahliaceae, $x = 6$. Saxifragaceae, sensu stricto, $x = 7$, with aneuploidy in several genera. *Chrysosplenium* does not fit well cytologically with the rest of the Saxifrageae-Leptarrheneae-Astilbeae, as it has $x = 12$ (11? 9?).

Crassulaceae very likely have $x = 9$, with early aneuploid reduction and some increase, together with the formation of secondary basic numbers such as $x = 17$, common in the family. *Sedum* has every gametic chromosome number from $n = 4$ to $n = 12$ inclusive.

Rosaceae have been much studied and discussed cytologically, primarily because it was realized early that the base number of subfamily Pomoideae was $x = 17$, and the group is therefore of paleotetrapoloid origin (Sax, 1931, 1933). In subfamily Prunoideae, including *Exochorda*, $x = 8$, and in Spiraeoideae $x = 9$. It has been suggested that Pomoideae might be of tetraploid origin from the stocks that eventually led to the evolution of these large groups, but this no longer appears to be likely, as there is evidently no direct relationship between Prunoideae and Pomoideae (W. G. D'Arcy, personal communication). In Rosoideae, $x = 7$ is the common base number, but x = 9 occurs in several lines, including the more primitive woody genera of Dryadeae and Kerrieae, and $x = 8$ is the base number in the subtribe Alchemillinae. Isolated groups of special interest within Rosaceae recently counted by Peter Goldblatt (1976c) include *Kageneckia*, $n = 17$ (all 3 species); *Quillaja*, $n = 14$ ($n = 17$ also reported, evidently in error); and *Vauqelinia* (3 species), $n = 15$. *Lyonothamnus*, another morphologically isolated genus, fits chromosomally into Spiraeoideae and with other relatively primitive roses with $n = 27$, which certainly does not suggest a close relationship with *Vauquelinia*. In view of this distribution, it seems possible that the original basic chromosome number of Rosaceae was $x = 9$, but there were certainly several instances of aneuploid reduction and perhaps increase, as well as the early polyploid origin of Pomoideae. Reduction to $x = 7$ in the evolution of Rosoideae must have taken place very early, considering the fact that Sanguisorbeae are common to Africa and South America, with woody, evidently relict genera on each continent; this might even be the original basic chromosome number for the family.

Of the families related to Rosaceae, Neuradaceae have $x = 7$ and Chrysobalanaceae $n = 11$ in three genera with $n = 10$ in *Parinari*. For Fabaceae,

Caesalpinioideae might have $x = 7$, with early polyploidy and reduction from $n = 14$ to $n = 11$. Base numbers of $x = 8$ occur in a few genera scattered through many groups, and seem to have arisen early also; $x = 10$ occurs in *Pterogyne*. Although $x = 8$ has been proposed as the original basic chromosome number of Papilionoideae by Senn (1938), and of Caesalpinioideae by Turner & Fearing (1959), $x = 7$ appears appears to be another possibility in view of the distribution of polyploid chromosome numbers of apparently relictual genera, especially in Caesalpinioideae (Turner & Fearing, 1959). Mimosoideae evidently have a basic chromosome number of $x = 7$, with the derived numbers $x = 13$ and 14 frequent, and $x = 8$ in several lines, but $n = 8$ apparently no longer represented. For Faboideae, $x = 7$ is common to all tribes except Phaseoleae and Dalbergieae, which have basic chromosome numbers that might in part at least be derived from $n = 14$; but many aneuploid derivatives, if the hypothesis of $x = 7$ as the original basic chromosome number is correct, have been established early in the history of the group.

Summarizing for Rosales, $x = 7$, 8, and 9 all appear candidates for the original basic chromosome number for the order, with an ultimate derivation from $x = 7$. Connaraceae, usually included with Rosales but allied by Cronquist (1968) with Sapindales, fit very well chromosomally in Rosales, with $n = 14$ in six genera, $n = 13$ in one. On the other hand, chromosomal evidence does not provide additional evidence for the placement of Crossosomataceae (Thorne, 1968) in Rosales any more than in Dilleniales (Cronquist, 1968; Takhtajan, 1969), or of Staphyleaceae here (Thorne, 1968) rather than in Sapindales (Cronquist, 1968; Takhtajan, 1969). No chromosome counts are available for Eucryphiaceae, Davidsoniaceae, Byblidaceae, Columelliaceae, or Alseuosmiaceae.

V-2. *Podostemales.*—Judging from three counts from as many genera, $x = 10$ for the only family of this order. There are 45 genera and 130 species in the group.

V-3. *Haloragales.*—For Haloragaceae and Hippuridaceae, $x = 7$. For Gunneraceae, with only *Gunnera*, $n = 17$, with two reports of $n = 12$ which require confirmation. The chromosomal information available concerning *Gunnera* supports its segregation as a distinct family (Thorne in Becker, 1973). For *Theligonum*, only genus of Theligonaceae, both $n = 10$ and 11 have been reported.

V-4. *Myrtales.*—Sonneratiaceae have $x = 12$ in *Duabanga* and $n = 9$ in one count from *Sonneratia*. Lythraceae probably have $x = 8$, which is also the basic chromosome number in most genera (S. A. Graham, personal communication), with $n =$ ca. 10 in *Lafoensia*, $n = 30$ in *Nesaea*, and $x = 5$ in *Lythrum*. For Penaeaceae, $x = 10$ as far as known at present. Thymelaeaceae very clearly have $x = 9$. Trapaceae consist only of *Trapa*, with $x = 12$. Myrtaceae definitely have $x = 11$ (Smith-White, 1959). Heteropyxidaceae, recognized and placed in Rhamnales by Hutchinson (1959), but submerged in Myrtaceae by most recent authors, has $x = 12$ like Rhamnales but also some Myrtales. *Punica granatum* L., one of the two species of the only genus of Punicaceae, has $n = 8$ with up to 3 B-chromosomes (Mehra & Gill, 1971; P. K. Khosla, personal communication). Onagraceae have $x = 11$, which is the only basic number in the most primitive tribe, Fuchsieae, and in Circaeeae, and is found in the least specialized taxa of

Lopezieae and Onagreae also. Other chromosome numbers in the family have been derived by descending aneuploidy. Melastomataceae, with some 240 genera and 3000 species, have been very inadequately sampled, despite the wide range displayed by the approximately 75 counts that have been reported for about 30 genera. For subfamily Memecyloideae, $x = 7$ in *Memecylon* and $n = 12$ in the only species of *Mouriri* examined to date; unfortunately *Axinandra*, phylogenetically critical (Meijer, 1972), has yet to be examined cytologically. For the rest of the family, it can only be said that $x = 14$, 12, and 9 are common basic numbers, with all gametic numbers from $n = 8$ to $n = 19$ represented in one or more genera. For Crypteroniaceae, if circumscribed as proposed by Beusekom-Osinga and Beusekom (1975), *Rhynchocalyx* has $n = 10$ (Goldblatt, 1976a). For Combretaceae, $x = 12$ is the most likely original basic chromosome number, with aneuploid increase in *Quisqualis* and *Combretum*. Reports of $n = 7$ and $n = 13$ in Indian species of *Terminalia*, as by Nanda (1962), have not been reconfirmed (P. K. Khosla, personal communication). One species of *Olinia* has $n = 12$ (Goldblatt, 1976a). For Myrtales as a whole, considering that $x = 12$ in Sonneratiaceae, Trapaceae, Oliniaceae, and Combretaceae, and that this might be the base for Melastomataceae, one might guess that either it or, less plausibly, $x = 11$, definitely the original basic chromosome number in Myrtaceae and Onagraceae, would be the original basic number. No counts are available for Dialypetalanthaceae.

V-5. *Proteales*.—For Proteaceae, $x = 7$ (Johnson & Briggs, 1963). Eleagnaceae, on the other hand, appear to have $x = 14$ in *Elaeagnus* and $x = 12$ in *Hippophaë*, and $x = 11$ (13?) in *Shepherdia*, from which $x = 7$ could be inferred for them also. In *Hippophaë*, $n = 6$ has been reported by Darmer (1947) but doubted by Rousi (1965, 1971); the existence of such a chromosome number should be checked at the original locality, Hiddensee in the Baltic. Chromosomal evidence tends to support Cronquist's (1968) and Takhtajan's (1969) alliance of these two families, but definitely is in conflict with a derivation from Thymelaeaceae or Myrtales, as it is very probably related directly to $x = 7$, the original basic chromosome number of angiosperms.

V-6. *Cornales*.—The monotypic Davidiaceae have $n = 21$ (P. Goldblatt, unpublished). Nyssaceae, Garryaceae, and Alangiaceae have $x = 11$, with $n = 21$ also in the monotypic *Camptotheca* (Nyssaceae; Perdue et al., 1970). Within Cornaceae, the monotypic southern African Curtisioideae have $n = 13$ (P. Goldblatt, unpublished); Mastixioideae $n = 13$ and 11 (P. Goldblatt, unpublished); and Cornoideae probably $x = 11$, with descending aneuploidy to $n = 9$ in the *Cornus* complex. Among the more distantly related genera assigned to this subfamily, *Aucuba* has $x = 8$, *Griselinia* $n = 18$, and *Helwingia* $x = 19$. The chromosome number of the Himalayan and west Chinese *Toricellia* is unfortunately unknown. The chromosome number of *Corokia*, $n = 9$, provides no evidence for its placement in Cornales or Saxifragales, although the arguments of Eyde (1966) for the latter disposition appear convincing.

For the order Cornales, the existence of $n = 13$ in *Curtisia* and at least one species of *Mastixia* suggests that $n = 13$, or possibly even $n = 14(7)$ might be the original basic chromosome number, with early reduction to $n = 11$. *Aucuba*,

Griselinia, and *Corokia* stand out as sharply chromosomally as they do morphologically. If the hypothesis as to original basic chromosome number for the order presented here is correct, it would be implied that Nyssaceae, Garryaceae, and Alangiaceae are more closely related to Cornoideae than are Curtisioideae and Mastixioideae.

It would be desirable to obtain chromosome counts of *Argophyllum* (Escalloniaceae) and of such genera as *Melanophylla* and *Kaliphora* as part of an investigation of their affinities. Rhizophoraceae have $n = 32$ in Macarisieae and $n = 18$ in Rhizophoreae, suggesting base numbers of $x = 8$ and 9, but not supporting a close relationship with either Cornales or Myrtales. They might better be placed with Myrtales (Takhtajan, 1969), as the Cornales are, on the whole, a more homogeneous order (R. Eyde, personal communication). On cytological grounds, Cornales ($x = 13$) appear distinct from Umbellales ($x = 6$), with which they were combined by Thorne (1968) and Takhtajan (1969); however, the orders are probably more closely related than is suggested by their wide separation in the system of Cronquist (1968).

V-7. *Santalales*.—Only six chromosome counts have been reported for Olacaceae, each for a separate genus; these indicate basic chromosome numbers of $x = 10$, 12, 13, and 19. The only count reported for Opiliaceae to date is $n = 10$. Santalaceae, which would amply repay further investigation, have $x = 5$, 6, 10, 12, 13, 19, and 36 in a very few scattered counts. Loranthaceae have $x = 12$ (Barlow & Wiens, 1971), with progressive aneuploid reduction, while Viscaceae have two groups, one with $x = 14$ and the other with $x = 10$, 11, 12, and 13 (Wiens & Barlow, 1971). Eremolepidaceae have $n = 13$ and $n = 10$ in the two available counts, each from a separate genus. In Balanophoraceae, one species each of the distantly related *Helosis* and *Thonningia* have $n = 18$, and one of *Balanophora* has $n =$ ca. 16; if the family is really heterogeneous and the result of convergent evolution (Airy Shaw, 1966), further cytological information would be highly desirable. The only count of Cynomoriaceae, made in 1903, was $n = 12$. No chromosome counts are available for Dipentodontaceae, Grubbiaceae, Medusandraceae, or Myzodendraceae. For the order as a whole, much more information is needed, particularly on Santalaceae, to determine whether chromosome numbers of $n = 5$ (*Santalum*) and $n = 6$ (*Thesium*) were derived by aneuploid reduction or reflect the original basic chromosome number for the family and order. At present, $x = 6$ might cautiously be advanced as the original basic chromosome number of the group, with $x = 12$ and $x = 18$ important polyploid derivatives.

V-8. *Rafflesiales*.—For Rafflesiaceae, $x = 12$, 10, and perhaps 8 ($n = 16$ in *Cytinus hypocistis* L.). *Mitrastemon*, treated by Cronquist (1968) as a distinct family, also has $x = 10$. Hydnoraceae have not been studied cytologically.

V-9. *Celastrales*.—Hippocrateaceae have $x = 14$, with $n = 30$ in *Hemiangium* (Bawa, 1973). Celastraceae, for which only 9 of 55 genera have been examined, have $x = 9$, 8, 10, 14, and 12 as important chromosome numbers; they should certainly be studied much more extensively cytologically. *Stackhousia* (Stackhousiaceae) has $x = 9$ and 10. The only count available for Salvadoraceae is $n = 12$. *Ilex*, the only one of the three genera of Aquifoliaceae for which information is available, has $x = 20$ (Frierson, 1959; F. S. Santamour, Jr., personal com-

munication). In four Himalayan species, $n = 18$, although most species from this region, like those from other areas, have $n = 20$ (Mehra & Khosla, 1969). Icacinaceae, for which counts are available for six of about 58 genera and seven of about 400 species, have $x = 10$ in four genera, and $n = 11$ and $n = 12$ in one each. Dichapetalaceae evidently have $n = 12$ (Gadella, 1972), based on counts from *Dichapetalum* only. No information is available concerning Geissolomataceae, Siphonodontaceae (Capusiaceae), or Cardiopterygaceae. Corynocarpaceae fit better here cytologically (Takhtajan, 1969) than in Ranunculales (Cronquist, 1968). If Celastrales constitute a homogeneous and monophyletic group, then the original basic chromosome number is likely to be $x = 12$, with early and important aneuploid reduction. As a close relationship with Santalales seems likely (Thorne, 1968, combines the orders), the meaning of $x = 6$ in Santalaceae assumes importance in understanding the evolution of the entire complex.

V-10. *Euphorbiales.*—Buxaceae have $x = 14$ (*Buxus*, *Sarcococca*), $x = 10$ (*Notobuxus*), $n = 13$, 27 (*Pachysandra*; G. Davidse, personal communication), and $x = 13$ (*Simmondsia*). Unfortunately, no count is available for *Styloceras*, the remaining genus, which has been grouped with *Notobuxus* in a tribe Stylocereae. For Euphorbiaceae, much more information is needed; fewer than 5 per cent of the approximately 7,000 species have been examined cytologically. Nevertheless, in the subfamily Phyllanthoideae, with $x = 13$ in the more primitive taxa (Webster, 1967), it seems highly likely that this is the original basic chromosome number. In the other and more diverse subfamily, Euphorbioideae (Crotonoideae) $x = 9$, 10, and 11 are the most frequent basic numbers, with the latter perhaps the most likely candidate for the original basic chromosome number, based on present evidence (G. L. Webster, personal communication). Despite the arguments of Hans (1973), there seems to be little basis for accepting $n = 7$ as one of the original basic chromosome numbers of Euphorbiaceae on present evidence. No information is available for the very distinct Australasian genera *Poranthera* and *Ricinicarpos* (Airy Shaw, 1966). Daphniphyllaceae have $n = 16$ (two species). For Pandaceae, only one count for *Microdesmis*, $n = 15$, is available; this number is unusual in Euphorbiaceae (Webster, 1967), and it would be interesting to have a determination of chromosome number for *Panda*. The monotypic Chilean Aextoxicaceae have not been examined cytologically. Webster (1967) considers the similarities between Euphorbiaceae and Buxaceae to be the result of convergent evolution, but chromosomal evidence provides a weak suggestion of $x = 7$ (or 14) in both. This is also an important basic chromosome number in Malvales and Urticales, related to Euphorbiales by Thorne (1968) and many other authors, but widely separated by Cronquist (1968).

V-11. *Rhamnales.*—Rhamnaceae have $x = 12$, with $x = 11$ in the tribe Colletieae and some aneuploidy in *Rhamnus*, sensu lato. The very distinct monotypic African *Maesopsis*, constituting a subfamily of its own, has $n = 9$, as does the only species of *Gouania* to be counted to date; their relationships should be studied further. Leeaceae, a monogeneric family, have $x = 12$, with one report of $n = 11$, and one of $n = 10$. Vitaceae have $x = 12$ with aneuploidy in *Cissus*, $x = 11$ and 13 in *Tetrastigma*, $x = 10$ in *Cayratia*, and $x = 20$ or 19 in other genera. The original basic chromosome number for this family, and for the whole order,

seems probably to be $x = 12$. Cytologically, these three families are similar, which accords with their long-assumed relationship (Takhtajan, 1969). They are widely separated by Thorne (1968), who allies the Rhamnaceae with a series of orders in which $x = 7$, and Vitaceae with Cornales in which $x = 11$.

V-12. *Sapindales.*—Staphyleaceae have $x = 13$, Melianthaceae $x = 19$ (18 also?), Greyiaceae $x = 17$ or 16 (Goldblatt, 1976a). Connaraceae have $n = 14$ in one count each for six genera and $n = 13$ in one count for a seventh genus, a pattern that would fit equally well here or in Rosales (Thorne, 1968; Takhtajan, 1969, as an order near Rosales). Sapindaceae, which will prove very interesting cytologically when better sampled, have basic numbers of $x = 11$, 12, 13 (Mehra & Khosla, 1969), 14, 15, and 16 in 23 of some 150 genera that have been examined. For the widespread *Dodonaea viscosa* Jacq., counts of $n = 14$, 15, and 16 have been reported. Hippocastanaceae are sharply distinct cytologically, with $x = 20$ in both genera. Aceraceae have $x = 13$. Burseraceae probably also have $x = 13$, with $n = 11$ and 12 the only two chromosome numbers reported for *Bursera*. In *Dacryodes*, the only count reported to date is $n = 23$. In Anacardiaceae, $x = 14$, 15, and 16 are common basic numbers, with $x = 12$ represented in several genera. *Mangifera* has $n = 20$, also reported for *Lannea* (another species has $n = 14$), and *Anacardium* seems to have $n = 21$. Both genera of Podoaceae, *Campylopetalum* and *Dobinea* (Mehra & Khosla, 1969), have $n = 7$, which strongly supports their segregation from Anacardiaceae as a distinct family. It seems justifiable, however, to conclude that $x = 7$ is the original basic chromosome number for Anacardiaceae, with most of the evolution proceeding at the tetraploid level. Simaroubaceae have $x = 14$, 13, and 12 commonly, with the first perhaps the original basic chromosome number. Rutaceae were considered by Smith-White (1959) to have an original basic chromosome number of $x = 9$, which stands in sharp contrast to all other Sapindales. Ehrendorfer (in press) in contrast, considers that $x = 9$ was derived by aneuploid increase from $n = 7$ early in the evolution of the family, and that its original base number is $x = 7$. Cneoraceae have $n = 18$. For Meliaceae (Styles & Vosa, 1971), $x = 14$, 13 (Mehra et al., 1972), and 12 are perhaps the lowest numbers determined with certainty, but $n = 8$ and 11 have been reported for two different species of *Sandoricum*, which should be studied in more detail. The single species that has been segregated as Aitoniaceae, *Nymania capensis* (Thunberg) S. O. Lindberg, has $n =$ ca. 24 (Goldblatt, 1976a). Zygophyllaceae have $x = 13$, judging from the distribution of this chromosome number in relatively primitive, woody genera, with descending aneuploidy in a number of genera, culminating in a base number of $x = 6$ in the advanced genus *Tribulus* (D. M. Porter, personal communication). Cytologically, Coriariceae ($x = 20$) fit much better here, where they are placed by Takhtajan (1969), than in Ranunculales (Cronquist, 1968). They are equally compatible with Rosales (Thorne, 1968). Summing up for Sapindales, $x = 7$, with early evolution of $x = 14$ and, from it, $x = 13$, as well as (in Rutaceae and Cneoraceae) $x = 9$. No information is available concerning Akaniaceae, Julianaceae, Stylobasiaceae, or Surianaceae.

V-13. *Geraniales.*—Within Oxalidaceae, the rather isolated, woody genus *Averrhoa* has $x = 12$ and 11. Amongst the herbaceous members of the family, $x = 9$ in *Biophytum*, and *Oxalis* has every gametic chromosome number from

$n = 5$ to $n = 12$ inclusive, with a mode at $n = 7$. Such a pattern would be consistent with an original basic chromosome number for the family of $x = 12$, with aneuploid reduction in the herbaceous groups, or with an original basic number of $x = 7$, with subsequent polyploidy and aneuploid change. The two genera of Geraniaceae with the least specialized flowers, *Sarcocaulon* and *Monsonia*, have $n = 22$ and $n = 12$ respectively, whereas *Erodium* may have $x = 10$ and *Geranium* $x = 14$. The most specialized genus, *Pelargonium*, has $x = 11$. *Balbisia*, one of the genera sometimes segregated as Ledocarpaceae, has $n = 9$. Limnanthaceae all have $n = 5$. Tropaeolaceae have $x = 14$, 13, and 12. Balsaminaceae consist of *Hydrocera*, possibly the more primitive genus, with $n = 8$, and *Impatiens* with $n = 6$–11 inclusive, the most common numbers being $n = 10$, 8, and 7 (Jones & Smith, 1966). For the order as a whole, it is almost impossible to guess whether the original basic chromosome number is $x = 7$, 12, or 14.

V-14. *Linales*.—For Erythroxylaceae, $n = 12$. The only determination of chromosome number available for Humiriaceae is likewise $n = 12$. In Linaceae, $n = 11$ and 10 in *Reinwardtia*; $x = 9$ in *Linum* (Harris, 1968), with aneuploid reduction to $n = 6$ in some species; $n = 18$ and 17 in *Hesperolinon*, and $x = 6$ in *Hugonia*. The last mentioned may indicate an original basic chromosome number of $x = 6$ for the order Linales as a whole.

V-15. *Polygalales*.—Only 35 chromosome counts, representing 12 genera, appear to be available for Malpighiaceae, a family of about 60 genera and 800 species. In *Galphimia* and *Lophanthera* $x = 6$, which implies that the numbers $x = 12$, 11, 10, and 9 are derived from it by polyploidy followed by aneuploid reduction, and that $x = 6$ is the basic chromosome number for the family. Polygalaceae have all gametic chromosome numbers from $n = 7$ to $n = 12$ in different genera, and in *Polygala* itself $n = 8$, 12, and 14–21 inclusive. In *Monnina*, $x = 5$. There seems to be no point in attempting to guess a basic chromosome number with the available information. Krameriaceae have $x = 6$. No information about the chromosomes of Trigoniaceae, Vochysiaceae, Tremandraceae, Xanthophyllaceae, or Polygalaceae tribe Moutabeae seems to have been published. For the order, $x = 6$ seems to be the original basic chromosome number, with some doubt as to the course of evolution in Polygalaceae.

V-16. *Umbellales*.—Araliaceae clearly have $x = 12$. *Helwingia*, placed here for example by Hutchinson (1959), has $x = 19$ and is very distinct cytologically. In Apiaceae, Apioideae have $x = 11$, with frequent descending aneuploidy, whereas Hydrocotyloideae and Saniculoideae have $x = 8$. It is possible that *Oreomyrrhis* (Mathias & Constance, 1955), one of the most distinct of the Apioideae, with $n = 6$ (one species has $n = 7$), retains the basic chromosome number of the order. For the order as a whole, I cautiously postulate a base number of $x = 6$, especially in view of the very close relationship between Apiaceae and Araliaceae (Thorne, 1973).

VI. SUBCLASS ASTERIDAE

VI-1. *Gentianales*.—In families that have been segregated from Loganiaceae, Antoniaceae and Strychnaceae have $x = 11$, Desfontainiaceae $n = 7$. Spigeliaceae

have $n = 10$ in *Cynoctonum*, $x = 8$ and 13 in *Spigelia*. Potaliaceae evidently have $x = 6$ in *Fagraea* and *Anthocleista* ($n = 24$ and $n = 30$ are the two reported numbers). In Loganiaceae, sensu stricto, $x = 11$, 10, and 8 are the basic chromosome numbers. In *Retzia*, probably most closely related to Loganiaceae, $n = 12$ (Goldblatt & Keating, 1976). In Gentianaceae, $x = 10$, 11, and 13 are the most common basic numbers, with aneuploid numbers below $n = 10$ having evidently been derived independently in several different lines. Both $x = 10$ and $x = 13$ occur, with other aneuploid numbers both in *Gentiana*, sensu stricto, and in *Swertia*. In the Brazilian *Deianira*, the only member of the South American tribe Helieae to be examined cytologically, $n = 7$, suggesting $x = 7$ for the family, with tetraploidy occurring early in its evolution. Apocynaceae have $x = 11$, with rather frequent descending aneuploidy in a number of lines to $n = 6$. Asclepiadaceae also have $x = 11$, but with aneuploidy much less common; a very high proportion of the species examined have had $n = 11$. The basic chromosome number for the order is probably $x = 7$, which seems to have given rise to $x = 6$ early in the history of the group. Presumably, $x = 11$ in Antoniaceae, Strychnaceae, and Apocynaceae-Asclepiadaceae have been derived independently from $x = 14$.

VI-2. *Polemoniales*.—Nolanaceae have $n = 12$. Solanaceae also have $x = 12$ with a good deal of aneuploid reduction in different lines, reaching $n = 7$ in *Petunia*. The original basic number of Convolvulvaceae may be $x = 7$, judging from its presence, together with $x = 14$ and $x = 15$, in *Cuscuta*; these latter two numbers are the most common in the family, suggesting perhaps the early presence of $n = 7$ and $n = 8$ and subsequent aneuploid reduction at the tetraploid level in the ancestors of *Porana* ($x = 13$), *Evolvulus* ($x = 13$, 12), *Calystegia* ($x = 11$), and within *Convolvulus* sensu stricto ($x = 15$, 14, 12, 11, 10) and *Merremia* ($x = 15$, 14, 11). Menyanthaceae have $x = 9$, and seem to fit better in this order cytologically than in Gentianales (Takhtajan, 1969). Polemoniaceae also have $x = 9$ (Grant, 1959). Hydrophyllaceae might also have a basic chromosome number of $x = 9$, if both aneuploid increase and decrease are assumed; this number does occur in several key groups, and the South African *Codon* has $n = 17$ ($9 + 8$?). Aneuploid increase would then be involved in the evolution of the *Phacelia magellanica* group, the miltitzioid phacelias, *Ellisia*, *Eucrypta*, *Romanzoffia*, and *Codon*, with polyploidy involved in the origin of *Turricula* ($n = 13$) and *Eriodictyon* ($n = 14$). Lennoaceae have $x = 9$ also. If this order is a monophyletic one, $x = 7$ is probably the original basic chromosome number, with aneuploid reduction at that level or from the tetraploid $n = 14$ to give rise to $x = 12$, early in the history of the group.

VI-3. *Lamiales*.—The original basic chromosome number of Boraginaceae seems to be $x = 12$, with aneuploid reduction very frequent and reaching $n = 4$ in *Arnebia* and one species of *Amsinckia*. Important basic numbers in Ehretioideae are $x = 10$, 9, and 8, with $n = 16$, 15, 14, 24, and possibly 21 represented in *Cordia* (Bawa, 1973). *Callitriche* (Callitrichaceae) has species with $n = 3$, 4, 5, 10 and higher numbers; $x = 5$ appears probable. Verbenaceae seem to have been insufficiently studied cytologically to make speculations about their original basic chromosome number profitable. The basic numbers $x = 7$ in *Verbena* sensu stricto, $x = 5$ in *Glandularia*, and the report of $n = 6$ in *Priva lappulacea* (L.) Pers.

almost certainly represent reductions. Otherwise, the only report of a chromosome number less than $n = 11$ in Verbenaceae is one of $n = 9$ for *Phyla nodiflora* (L.) Greene. On the other hand, numbers such as $n = 11$, 12, 13, 14, 15, 16, 17, and 18 are well distributed among the genera for which information is available, with evident aneuploid change in such genera as *Callicarpa* ($x = 16$, 17, 18), *Gmelinia* ($x = 18$, 19, 20), and *Vitex* ($x = 12$, 13, 15, 16, 17). *Nyctanthes*, a very distinctive genus usually included in Verbenaceae, has $n = 23$ like many genera of Oleaceae, another family with which it has been allied. Kundu & De (1968) have concluded that it may best be recognized as a distinct family near Oleaceae. The monotypic Phrymaceae have $n = 14$, although Sugiura (1936) has been misquoted as having reported $n = 7$, which he did not.

In the large family Lamiaceae, counts are available for nearly half of the 180 genera, but only a very low proportion of the 3500 species. With the help of Briquet's (1895) invaluable treatment, some order may be brought out of the rich diversity of chromosome numbers reported to date. In the clearly most primitive subfamily Ajugoideae, $x = 14$, the most common basic number in *Ajuga*, may be the basic number, although $n = 16$ and $n = 31$ are also represented in the genus; for other genera of the subfamily that have been examined cytologically, $x = 13$ in *Amethystea*; $x = 12$ in *Rosmarinus*; $x = 10$ in *Trichostema*, with subsequent aneuploid reduction in the annuals to $x = 7$ (Lewis, 1960); $x = 9$ in *Teucrium*; and $x = 16$ ($= 8$?) in *Tunnea*. Much aneuploid reduction in chromosome number has taken place in the more advanced subfamily Ocimoideae, with reduction to $x = 7$ in three separate tribes, and in Stachyoideae, also with reduced chromosome numbers in three tribes. The Nepeteae will serve to illustrate these reductions; in *Agastache*, *Meehania*, and *Glechoma*, $x = 9$; in *Nepeta*, $x = 9$ and 8; in *Lallemantia*, $x = 7$; in *Schizonepeta*, $x = 6$; and in *Dracocephalum*, $x = 7$, 6, and 5—$n = 5$ in this genus being the lowest chromosome number yet recorded in the family. Unfortunately, no chromosome counts seem to be available for the primitive Australian subfamily Prostantheroideae, which will be helpful in testing the hypothesis of $x = 14$ as the original basic chromosome number for the family Lamiaceae. The original basic chromosome number of Lamiales might also be $x = 14$, with reduction to $x = 12$ in the ancestor of Boraginaceae.

VI-4. *Plantaginales*.—Plantaginaceae, the only family, seem clearly to have $x = 6$.

VI-5. *Schrophulariales*.—Buddlejaceae have $x = 19$, which accords with their distinctiveness from Loganiaceae. Oleaceae (Johnson, 1957) have $x = 11$ (*Menodora*) and $x = 13$ (*Jasminum*) in the tribe Jasmineae; $x = 13$ in *Fontanesia*, the only genus of Fontanesieae; and $x = 14$ in both genera of Forsythieae. These tribes belong to the subfamily Jasminoideae. In the other subfamily, Oleoideae (including Schrebereae; Briggs, 1970), $x = 23$ with aneuploidy in *Syringa*, *Osmanthus*, and *Phillyrea*, and $n = 20$ the only chromosome number reported for *Haenianthus* (Nevling, 1969). Two African species of the closely related *Linociera* also have $n = 20$, a chromosome number otherwise unknown in the family, whereas two species from New Caledonia have $n = 23$. This suggests that African species of *Linociera* may have had a common ancestor with *Haenianthus*. As suggested by Taylor (1945), $x = 14$ is probably the original base number in

Oleaceae, with $x = 23$ formed following aneuploid reduction to $n = 12$ and $n = 11$. Chromosome counts of the remaining unexamined members of Jasminoideae, *Comoranthus*, *Noldeanthus*, and especially *Myxopyrum*, would be especially interesting.

Scrophulariaceae are extremely diverse cytologically, and the overall pattern is difficult to determine. Many of the tribes appear to be characterized by descending aneuploidy, but it is not certain whether any of the original diploids persist in most of them or not. For example, in Digitaleae, $x = 14$ would appear reasonable, but the monotypic European *Erinus* has $n = 7$; in Cheloneae, $x = 14$ also appears reasonable, but *Collinsia*, perhaps an advanced genus, has $x = 7$; in Rhinantheae, $x = 12$ seems reasonable, but there is a doubtful report of $n = 6$ for *Bartsia alpina* L., which otherwise has reports of $n = 12$, $n = 14$, and $n = 18$; and in Gratioleae, *Gratiola* and *Lindernia* could be interpreted as having descending aneuploid series to $n = 7$, but the only species of *Dopatrium* examined has $n = 7$ also. Hemimerideae seem to have $x = 14$, 12, 10, and 9, and Verbasceae, with rotate corollas, have an inferred $x = 10$, 9, and 8. Perhaps the most important clue comes from the very distinct South African Selagineae, which have even been segregated as a distinct family; both species counted, in two different genera, have $n = 7$. This group has been added to Globulariaceae, which have $x = 8$, by Cronquist (1968), and both are related to Scrophulariaceae-Manuleae, which have $x = 6$. On the balance, $x = 7$ is assumed to be the original basic chromosome number for Scrophulariaceae.

Myoporaceae have $x = 9$, based on $n = 54$ in *Myoporum laetum* Forst. f. and $n = 18$, 36, and 54 in *Eremophila*. Globulariaceae have $x = 8$.

Despite information on about half of the approximately 120 genera, it is difficult to postulate an original basic chromosome number for Gesneriaceae (Moore & Lee, 1967; Ratter, 1975). Considering the mainly New World subfamily Gesnerioideae first, $x = 9$ is probable for the Columneeae, which have a superior ovary and both terrestrial and epiphytic habits, and some of the apparently more advanced genera have $x = 8$ (H. E. Moore, Jr., personal communication). In the epiphytic Gesnerieae, $x = 7$, with $n = 7$ recently reported for *Gesneria sintenisii* Urb. (Nevling, 1969). In other tribes, $x = 13$ and 11 are frequent, $x = 12$ and 10 less so. The interpretation of $n = 16$ in *Besleria* is not clear at present, but it is perhaps tetraploid based on $x = 8$. In the mainly Old World subfamily Cyrtandroideae, $x = 10$ is found in certain genera of Cyrtandreae, Klugieae, and Didymocarpeae (Burtt, 1962), with $x = 8$, 9 and apparent multiples widespread in all four tribes. The numbers $n = 8$, 9 and apparent multiples widespread in all four tribes. The numbers $n = 8$ and 9 are likewise represented in the large genera *Chirita*, *Didymocarpus*, and *Boea*, which have various aneuploid and polyploid derivatives also. In summary, $x = 9$ may be the original basic chromosome number for Gesnerioideae and $x = 8$ or 9 for Cyrtandroideae (B. L. Burtt, personal communication; Ratter, 1975). This suggests $x = 9$ as the original basic chromosome number for the family, particularly if the two subfamilies are actually directly related to one another.

Orobanchaceae have $x = 12$ and 19 in *Orobanche* and $x = 18$, 19, 20, and 21 in some other genera; a very tentative suggestion of $x = 7$ for the family might be

deduced from these numbers. In Bignoniaceae, $x = 20$ is by far the most frequent base number in all tribes, and the only one known in the less diverse tribes Crescentieae and Tourrettieae. Significantly, *Oroxylum*, the only one of the presumably most primitive genera of the family (those with five fertile stamens) which has been counted, has $n = 14$ ($n = 15$ also reported), which, taken together with the frequent occurrence of $n = 20$, suggests $x = 7$ as basic to the family. *Millingtonia* has $n = 15$, but most other chromosome counts deviating from $n = 20$ should be reconfirmed. The most derived herbaceous genera, however, have some of the lowest chromosome numbers ($n = 11$ in *Incarvillea*, $n = 15$ in *Argylia*), which might be derived by aneuploidy at the tetraploid level. In Acanthaceae, the relatively few chromosome counts that have been made reveal a great diversity; $x = 14$ and $x = 21$ are frequent, as are other basic numbers from $x = 8$ to $x = 17$. On the basis of very limited evidence, $x = 7$ is suggested as the original basic chromosome number for Acanthaceae, as tentatively proposed by Grant (1955). In Pedaliaceae, sensu stricto, $x = 8$ and 13, and in Martyniaceae, $x = 15$ and 16. Lentibulariaceae have $x = 11$, 8, and (in one species) 6 in *Pinguicula*; $x = 6$, 7, 9, 10, 14, 15, 18, and 21 in *Utricularia*; and $n = 9$ in *Orchyllium*. Hydrostachyaceae are known only from a 1915 count of $2n = 20$–24. For Scrophulariales as a whole, $x = 7$ seems possible, although much work remains to be done, and the original basic chromosome number might also have been $x = 8$, 9, or 10. Oleaceae and Buddlejaceae have had polyploid origins.

VI-6. *Campanulales.*—Sphenocleaceae have $n = 12$. In Campanulaceae, $x = 7$ in the subfamily Lobelioideae, with only a few deviating counts, but considerable aneuploidy in *Downingia*. The subfamily Campanuloideae exhibits considerable cytological diversity, with $x = 7$ still probably the original basic chromosome number. In *Campanula*, a large and diverse genus with many satellite genera, gametic chromosome numbers of $n = 7$–12 inclusive, as well as $n = 14$, 15, and 17, with various multiples, occur. In *Phyteuma*, $n = 10$–14 and 17 occur. Several genera related to *Campanula* have $x = 17$, and it eventually should be possible to work out the chromosomal phylogeny of the group in elegant detail. Even though *Specularia* has $x = 7$, 8, and 10, and *Peracarpa* has $n = 15$, it is likely that most chromosome numbers in the subtribe Campanulinae (all genera mentioned thus far) between $n = 8$ and $n = 13$ have been derived by aneuploid reduction from $n = 14$. In the Cyphioideae, *Nemacladus* has $x = 9$ (W. L. Bloom, personal communication). The two counts available for Stylidiaceae, each from a different genus, have been $n = 15$. The monotypic Australian Brunoniaceae have $x = 9$. Goodeniaceae, another mainly Australian family, have $x = 8$ in six genera; $x = 9$ in three, including *Leschenaultia*, *Dampiera*, and *Anthotium*; and $x = 7$ in three species of *Goodenia*, which otherwise has $x = 8$. Peacock (1963) considered it impossible to say whether $x = 8$ or 9 was the original basic number, but stated that $x = 7$ was clearly derived from $x = 8$. Cytologically, Brunoniaceae and Goodeniaceae do not seem closely related to Campanulaceae or Stylidiaceae, which would be in agreement with the observations of Carolin (1960).

VI-7. *Rubiales.*—As summarized by Verdcourt (1958), the cytological information available concerning Rubiaceae suggests that $x = 11$ is the original basic chromosome number, with reduction in several lines. On the other hand, the

presence of $x = 14$ in the morphologically advanced Spermacoceae and of $x = 12$ in *Catesbaea*, *Hamelia*, and *Hoffmannia*, not primitive genera, suggests aneuploid increase. Cytologically, the family would fit well in Gentianales, where it is placed by Thorne (1968) and Takhtajan (1969). The evidence would also agree well with a derivation of Rubiaceae from Loganiaceae (Cronquist, 1968: 87).

VI-8. *Dipsacales*.—Caprifoliaceae have $x = 9$ with $x = 8$ in some genera. Adoxaceae have $n = 18$ and possibly higher polyploid numbers in the single species. Valerianaceae have $x = 8$, but with $n = 11$ in *Patrinia*, one of the two genera with four stamens; the relationship of this number to $x = 8$ remains to be determined. In *Valeriana* in which $x = 8$ predominates, two species have $n = 12$. Dipsacaceae have $x = 9$ (Ehrendorfer, 1964), with much aneuploid reduction in the evolution of various genera. Calyceraceae have not been well sampled, but have $n = 8$, 15, 18, and 21 in the counts reported so far. For the order as a whole, $x = 9$ without much doubt.

VI-9. *Asterales*.—Asteraceae have $x = 9$ (e.g., Stebbins et al., 1953; Raven et al., 1960; Raven & Kyhos, 1961; Solbrig et al., 1964) with a great deal of aneuploidy and polyploidy.

Class Liliopsida (Monocotyledoneae)

I. subclass alismatidae

I-1. *Alismatales*.—Limnocharitaceae have $x = 10$, 8, and 7 in different genera, whereas the monotypic Butomaceae have $x = 13$. In Alismataceae, $x = 7$ and 11 are both important basic numbers.

I-2. *Hydrocharitales*.—Hydrocharitaceae have $x = 8$, 7, and 11 as frequent basic numbers, with considerable aneuploidy indicated by the published reports.

I-3. *Najadales*.—Aponogetonaceae have $x = 8$, the ditypic Scheuchzeriaceae $n = 11$, Juncaginaceae $x = 6$ (including *Lilaea*), Najadaceae $x = 6$, Potamogetonaceae $x = 7$ and $x = 13$, Ruppiaceae $x = 10$, Zannichelliaceae $x = 6$, and Zosteraceae $x = 6$ and 7.

I-4. *Triuridales*.—Counts of $n = 14$, 22, and 24 have been reported for different species of *Sciaphila* (Triuridaceae); no information is available for Petrosaviaceae.

II. subclass commelinidae

II-1. *Commelinales*.—The only count available for Rapateaceae is for the single African species, *Maschalocephalus dinklagei* Gilg & K. Schum., $n = 11$. *Xyris* (Xyridaceae) has $n = 9$ (North American species), 13 (six Australian species), and 17 (one Asian, one African species), with a dubious 1914 report of $n = 16$. Mayacaceae are unknown cytologically. Commelinaceae (Jones & Jopling, 1972) have an exceptionally wide range of chromosome morphology, and have basic chromosome numbers ranging from $x = 4$ to $x = 20$. In the Old World and pantropical genera, $x = 8$ and $x = 9$ are frequent base numbers, whereas in the New World genera, $x = 6$ and $x = 8$ are common. No original basic chromosome number or satisfactory scheme for chromosomal evolution in the family has been proposed.

II-2. *Eriocaulales*.—For Eriocaulon, $x = 8$ is the more common basic number, but $n = 10$ occurs in *E. compressum* Lam. No other genus of Eriocaulaceae has been examined cytologically.

II-3. *Restionales*.—*Flagellaria* (Flagellariaceae) has $n = 19$ (three species). In the Australasian members of the Restionaceae, $x = 6$ or 12 and $x = 11$ are frequent, with $x = 13$, 9, 7, and 16 also represented. As $x = 11$ and $x = 7$ are important basic chromosome numbers, at least among the Australian species of the family (Briggs, 1963) and since $x = 12$ and $x = 6$ occur in several genera that are not closely related (Briggs, 1966, personal communication), it is tentatively suggested that either $x = 6$ or 7 might be the original basic chromosome number for the family, with early tetraploidy followed by aneuploid reduction. On the other hand, *Hypodiscus aristatus* Nees, the only African species of the family for which chromosomal information is available, has $n = 16$ (Krupko, 1962), and further studies are clearly necessary. *Anarthria*, segregated by Cronquist (1968) as a separate family, has $x = 11$ and fits in cytologically with the rest of Restionaceae, whereas no information is available concerning Ecdeiocoleaceae. Centrolepidaceae, poorly sampled, have $n = 13$ and 10. For the order, $x = 7$ could be considered a likely candidate as the original basic chromosome number.

II-4. *Juncales*.—For *Luzula*, $x = 6$, and for *Juncus*, $x = 20$, with descending aneuploidy in some specialized groups. The very low number $n = 3$ in *Luzula* must clearly be derived also. They are the only genera of Juncaceae examined cytologically. Thurniaceae are unknown in this respect.

II-5. *Cyperales*.—At least some genera of Cyperaceae have polycentric chromosomes, and all numbers from $n = 5$ to 20 and above are represented in one or more species. The chromosomal situation in this family is similar to that in *Juncus*. Poaceae have $x = 12$, judging from the prevalence of this number among Bambuseae, if the scattered morphologically advanced genera with $x = 6$ in other tribes have been derived by aneuploid reduction, as appears probable. The interpretation of $x = 7$ in festucoid tribes (Brown & Smith, 1972) is problematical, but this number has in all likelihood been achieved by aneuploid reduction.

II-6. *Typhales*.—Both Typhaceae and Sparganiaceae have $x = 15$.

II-7. *Bromeliales*.—Marchant (1967) found $x = 25$ to be characteristic of most Bromeliaceae. *Cryptanthus* has $x = 17$, earlier reports of $x = 18$ evidently being in error. In *Aechmea tillandsioides* (Mart. ex Schult. f.) Baker, Marchant (1967) found $n = 21$, and suggested that it might have arisen through a combination of $n = 25$ and $n = 17$ at some early date. Subsequently, Sharma & Ghosh (1971) have reported $n = 23$, 24, 26, 27, and 49 in various members of the family and $n = 18$ in addition to $n = 17$ in *Cryptanthus*; all such records need careful evaluation and reconfirmation.

II-8. *Zingiberales*.—In Strelitziaceae, *Ravenala* and *Strelitzia* both have $n = 11$, with most species of the latter having $n = 7$. Both species of Lowiaceae have been examined cytologically, and had $n = 9$. *Heliconia*, only genus of Heliconiaceae, has $n = 12$ and $n = 11$ and, should they be confirmed, other chromosome numbers derived from them. Musaceae have $n = 9$, 10, and 11 as equally feasible candidates for original basic chromosome number (Simmonds, 1962). Costaceae have $x = 9$. Zingiberaceae have $x = 11$ and 12 as important basic chromosome numbers, but

also $n = 10$ (*Caulokaempferia*), and $x = 13$, 14, 16, 17, as well as higher numbers, in other genera. Cannaceae have $x = 9$. Marantaceae have $x = 11$, 12, 13, and 14, as well as $x = 4$, 6, 8, 9, and 10, as common basic numbers. Looking at the order as a whole, it is most likely that $x = 11$ could have been the original basic number (Mahanty, 1970).

III. SUBCLASS ARECIDAE

III-1. *Arecales.*—Arecaceae apparently have an original basic chromosome number of $n = 18$ (Moore & Uhl, 1973; R. W. Read, personal communication), judged from its presence in coryphoid, phenicoid, and some genera of arecoid and borassoid palms. Reduced chromosome numbers are found in a number of lines, with $n = 17$ occurring widely, and $n = 16$, 14, and 13 also represented.

III-2. *Cyclanthales.*—In the three species of *Carludovica* that have been studied cytologically, $n = 9$, 15, and 16 occur, suggesting that further studies may be very interesting.

III-3. *Pandanales.*—The basic chromosome number is clearly $x = 30$, with some aneuploidy. This would be in agreement with the notion of a relationship with Typhales, as indicated by the arrangements of Takhtajan (1969) and to some extent Thorne (1968).

III-4. *Arales.*—In Araceae, the preponderance of species with $n = 14$ and 21, coupled with other important base numbers such as $x = 13$ and 12, suggests $x = 7$ as the original basic chromosome number. There is, however, no species of the family with $n = 7$. As far as known, Lemnaceae have $n = 15$, 20, 21, 22, 25, 28–30, 35, and 40; the first four numbers might be consistent with a hexaploid origin on $x = 7$. *Pistia*, the genus of Araceae often cited as transitional to Lemnaceae, has $n = 14$.

IV. SUBCLASS LILIIDAE

IV-1. *Liliales.*—Philydraceae have $n = 8$ and $n = 17$. Pontederiaceae have $x = 8$ (*Pontederia, Eichhornia*) and 7 (*Monochoria*; also $n = 20$ and 26), as well as 15 (*Heteranthera*). For the large complex of genera and tribes treated by Cronquist (1968), Thorne (1968), and others as Liliaceae, cytological information has been extremely useful in the grouping of genera into suprageneric taxa. For example, the grouping of *Yucca* and *Agave*, originally placed in separate families but with an utterly distinctive gametic chromosome complement consisting of 5 large and 25 small chromosomes, has become a classical example of the use of cytological data in higher classification (McKelvey & Sax, 1933). The extension of this pattern to other genera, however, becomes more and more ambiguous (Darlington, 1956: 96–100), leading to doubts about the constitution of the family Agavaceae (Cronquist, 1968: 358), and even its abandonment owing to uncertainty about limits (Thorne, 1968). When available chromosomal information on *Liliaceae*, in the broad sense, is arranged according to the small and therefore presumably more or less natural tribes of Hutchinson (1959), no obvious original basic chromosome number emerges for the group as a whole, although all basic numbers from $x = 7$ to $x = 11$ are well represented. The general observation may be made that the tribes traditionally considered as Amaryllidaceae appear to have

an original basic chromosome number of $x = 12$ (or possibly 11), with reduction to $x = 7$ in Narcisseae, and that the Allieae, with $x = 9$, 8, 7, 6, and Agapantheae, with $x = 6$ and 15, appear slightly discordant in this group, where they have been placed by Hutchinson. What is known about the cytology of Iridaceae does not readily suggest an original basic chromosome number for the family (Goldblatt, 1971). It is of interest that Hutchinson's (1959) Hemerocalloideae, considered by him transitional to Amaryllidaceae, have basic chromosome numbers of $x = 11$, 12, and 14, like those of many Amaryllidaceae. Unfortunately, the critical tribes Isophysideae (Iridaceae) and Aphyllanthideae (Liliaceae) are unknown cytologically. Xanthorrhoeaceae have $n = 11$. Agavaceae have $x = 30$, 19, 12, and other basic numbers depending upon the composition of the group. Velloziaceae are known only from two 1925 counts of $n = 26$ and ca. 24 of the African *Talbotia elegans* Balfour, and from unpublished counts of $n = 9$ for *Vellozia* and $n = 16$ for *Barbacenia* (P. Goldblatt, personal communication) among the South American genera. Haemodoraceae have $n = 6$, 8, and 15, as well as $n = 7$, 5, and 4 (in *Conostylis*); no counts are available from the tribe Haemodoreae. Tecophilaeaceae, grouped by Cronquist (1968) with Haemodoraceae, have $x = 12$ and 10. Taccaceae have $n = 15$, based upon a single count. Stemonaceae have $n = 7$, also based upon a single count. Smilacaceae have $x = 13$, 15, and 16. Dioscoreaceae have $x = 10$, 12, 13, and 18. Both $n = 11$ and 12 have been reported for the same species of Cyanastraceae. Although chromosomal information will continue to be useful in the classification of suprageneric taxa in Liliales, it does not appear justifiable at present to attempt to deduce an original basic chromosome number for the order. Studies such as that of Huber (1969) will probably eventually point the way to a clarification of the evolutionary patterns in the group.

IV-2. *Orchidales.*—Although chromosomes will eventually prove useful in the classification of Orchidaceae (e.g., Jones, 1967), it would be premature to attempt to outline the pattern of evolution in the group or to suggest an original basic chromosome number. Burmanniaceae are very poorly known cytologically, with $x = 6$ a possible basic chromosome number based upon current information. Corsiaceae and Geosiridaceae are unknown cytologically.

DISCUSSION

A combination of chromosome number and morphology has proved useful in the classification of many families, as in the Rosaceae and Agavaceae discussed above. Another outstanding example is Gregory's (1941) study of Ranunculaceae, in which some genera have large chromosomes and $x = 8$; others small chromosomes and $x = 7$; and *Coptis* and *Xanthorrhiza* small chromosomes and $x = 9$. The cytological distinctiveness of *Paeonia*, with $x = 5$ and very large chromosomes, and of *Glaucidium* ($n = 10$) and *Hydrastis* ($n = 13$), with small chromosomes, was also demonstrated as a result of Gregory's pioneering study. Although Paeoniaceae is generally now recognized as a family only distantly related to Ranunculaceae, Hydrastiaceae generally are regarded as synonymous with Ranunculaceae. Cytological evidence favors their segregation.

In Onagraceae, Kurabayashi et al. (1962) demonstrated marked differences in the mitotic cycle of contraction in different tribes. Fuchsieae, Circaeeae, and

Lopezieae have large, relatively undifferentiated, slowly contracting chromosomes; Onagreae medium-sized ones with presumably strongly contracted, heterochromatic segments near the centromeres; and Jussiaeeae and Epilobieae small, tightly contracted ones that remained visible throughout interphase. Genera with the original basic chromosome number of the family, $x = 11$, occur in the first four of these tribes, with a considerable degree of aneuploid reduction in Lopezieae and Onagreae. Jussiaeeae have $x = 8$, Epilobieae $x = 9$, 10, 12, 13, 15, 16, and 18.

For the deduction of an original basic chromosome number in a family, a necessary step before comparisons can be made with other groups, a wide knowledge of phylogeny in the group is a necessary prerequisite. Outstanding studies that have analyzed complex situations and arrived at a solution to this problem include those of Johnson & Briggs (1963) on Proteaceae; those of Smith-White (1959) for various families; those of Barlow & Wiens (1971) on Loranthaceae; Grant (1959) on Polemoniaceae; Walker (1971, 1972) on Annonaceae; and the classical studies of Sax (1931, 1933) on Rosaceae. For a number of families, including Commelinaceae (Jones & Jopling, 1972), Orchidaceae, Liliaceae, Dilleniaceae, Lythraceae, Melastomataceae, and Acanthaceae, deductions about the original basic chromosome number are premature. In many small families, on the other hand, the original basic chromosome number is obvious, as it is in families that are relatively uniform cytologically, such as Apocynaceae, Cactaceae, Magnoliaceae, and Araliceae. Finally, in a number of families, the sort of detailed comparison of phylogeny with chromosomal information has not yet been made which would permit a truly critical evaluation of the original basic chromosome number but enough knowledge is available to permit a suggestion in this respect. Such suggestions have been made consistently in this paper so that they can be tested as more information about the plants concerned becomes available.

THE PATTERN IN MAGNOLIOPSIDA (DICOTYLEDONEAE)

A general review of the basic chromosome numbers and what they reveal about phylogeny in Cronquist's (1968) subclasses now seems in order. Darlington & Mather (1949: fig. 82; Darlington, 1956) attempted to provide a diagram of the relationships between basic chromosome numbers of woody dicots, but were hampered by many of the kinds of difficulties mentioned above. They accepted Hutchinson's (1959) phylogenetic relationships between the families.

I. *Magnoliidae*.—For this group, which has already been discussed in some detail, $x = 7$ is a plausible basic chromosome number at the ordinal level throughout. This would imply a basically tetraploid origin for Saururaceae and Piperaceae and could be used to argue for the exclusion of Coriariaceae and Corynocarpaceae from this line. It might also be used to argue for an ultimately tetraploid origin for Papaverales ($x = 10$?), although the point cannot be settled with present evidence.

II. *Hamamelididae*.—The original basic chromosome number can logically be inferred to have been $x = 7$, although the great majority of the families are of polyploid origin. A common basic number is also $x = 7$, with $x = 20$, 17, 16 and perhaps also 19 and 15 represented. By analogy with Magnoliidae, $x = 12$, which

is also frequent, might have been derived by aneuploid reduction from $x = 14$, as seems clearly to have been the case in Fagales. The presence of $x = 12$ and $x = 16$ as the two basic chromosome numbers in Hamamelidaceae is anomalous and requires explanation. In Urticales, $x = 14$ was the original basic chromosome number but the group might better be moved to a position near Malvales in the dilleniid line. The presence of $x = 16$ in Leitneriales, Juglandales, and Myricales, which traditionally have been associated on morphological grounds, indicates that they may well have been derived from a common ancestor with this number. They are probably better referred to Rosidae, as implied by the classification of Thorne (1968). Polyploidy and aneuploid increase to $n = 8$ both seem to have been early events in the evolution of Hamamelididae. Similar trends seem to have occurred both in Hamamelidaceae and in Betulaceae.

III. *Caryophyllidae*.—The most important basic number is $x = 9$, presumably derived by aneuploid increase from $x = 7$ in the common ancestor of the group, as well as $x = 12$ and 11 in Basellaceae, $x = 11$ in Cactaceae, and $x = 14$ in Caryophyllaceae. Polygonales have $x = 10$, 11, or 12, which suggests reduction from $x = 14$ and might be taken as being in agreement with the suggestion that they are quite distinct from other Caryophyllidae. Plumbaginaceae probably have $x = 7$, and Bataceae have $n = 9$.

IV. *Dilleniidae*.—Here, again, $x = 7$ is rather clearly the original basic chromosome number, with aneuploidy and tetraploidy early events. Capparales appear to have had a tetraploid origin, with $x = 14$ and descending aneuploidy, as do Ebenales (ancestor may have had $x = 12$) and Primulales ($x = 12$?). The orders Ericales and Diapensiales have $x = 6$, suggesting an alternate hypothesis for the origin of Ebenales and Primulales. Cytological evidence seems not to favor Thorne's (1968) removal of Diapensiales to the Rosales, although there is other evidence for such a disposition. Salicales have $x = 19$ $(12 + 7)$, and are therefore of paleohexaploid origin. Paeoniaceae have $x = 5$.

V. *Rosidae*.—Possibly $x = 7$, but with many early and important evolutionary changes. In Rosales, both Rosaceae and Crassulaceae have $x = 9$, and are possibly derived from a common ancestor with this chromosome number. Myrtales have apparently the unusual basic chromosome number of $x = 12$, whereas the probably related Cornales have $x = 11$. Rhizophoraceae ($x = 18$, 32) seem discordant in both groups, as do Thymelaeaceae, with $x = 9$. For Santalales, $x = 6$, which might might also suggest the original basic chromosome number of the closely related Celastrales and Rhamnales, in which otherwise a tetraploid origin with $x = 12$ is suggested. Linales, Polygalales, and Umbellales all seem to have $x = 6$. Rutaceae are unusual in Sapindales ($x = 7$) and in the subclass, with $x = 9$ probable.

VI. *Asteridae*.—The original basic chromosome number for most orders seems again to have been $x = 7$, with early tetraploidy and subsequent aneuploid reduction. Lamiales evidently have had a tetraploid origin, with $x = 14$. Plantaginales have $x = 6$, with Brunoniaceae $x = 9$, and Goodeniaceae $x = 8$, 9. Rubiales may have $x = 11$, Dipsacales and Asterales $x = 9$.

As may be seen from the preceding review, $x = 7$ in each subclass of this class except Caryophyllidae, in which $x = 9$ for the most part. Magnoliidae and

Hamamelididae have a high proportion of families that probably had a polyploid origin, the other four subclasses fewer. Reduced basic chromosome numbers of $x = 6$ are characteristic of Ericales and Diapensiales (Dilleniidae); of Santalales, Linales, Polygalales, and Umbellales (Rosidae); and of Plantaginales (Asteridae). In each of these groups, tetraploids are much more common than diploids. Basic chromosome numbers reduced still further, to $x = 5$, seem to be characteristic of only four families: Paeoniaceae, Frankeniaceae, Limnanthaceae, and Callitrichaceae. These families are unrelated.

Order of dicots that seem to have had a polyploid origin are Nymphaeales ($x = 12$–14, if the very distinct *Nelumbo*, $x = 8$, is excluded); Trochodendrales ($x = 19$), Eucommiales ($x = 17$), Urticales ($x = 14$), Leitneriales ($x = 16$), Juglandales ($x = 16$), and Myricales ($x = 16$) of the Hamamelididae; Lecythidales (poorly sampled; $x = 13, 16, 17, 18$) and Salicales ($x = 19$) of the Dilleniidae; and Lamiales ($x = 14$) of the Asteridae. Other orders which might have had a polyploid origin are Polygonales ($x = 12$, 11, or 10), Capparales ($x = 12$, 11, or 10), Primulales ($x = 12$), Myrtales ($x = 12$), Celastrales ($x = 12$), and Cornales ($x = 11$). Additional information will probably clarify the situation in many of these groups.

It has long been realized that some families and subdivisions of families were of polyploid origin. More than 40 years ago, Karl Sax (1931, 1933) demonstrated that the subfamily Pomoideae of Rosaceae, with $x = 17$, was a paleopolyploid based upon $x = 9$, the original basic chromosome number for Rosaceae, and $x = 8$. Comparable subfamilial groups of paleopolyploid origin include Oleaceae—Oleoideae, $x = 23$ (Taylor, 1945); Bromeliaceae except for *Cryptanthus*, $x = 25$ (Marchant, 1967); Fabaceae—Mimosoideae, $x = 14$; most Bignoniaceae, $x = 20$; and a series of genera related to *Campanula* (Campanulaceae), $x = 17$. That polyploidy should be frequent in the origin of such groups, and of families, should not be surprising; Grant (1963: 486) has estimated that some 47% of the species of angiosperms are of polyploid origin.

Among the Magnoliales, all of the families have been sampled cytologically. Three of these have ambiguous basic chromosome numbers ($x = 10$, 11). Of the remaining 20, only two—Annonaceae and Trimeniaceae—had a diploid origin. Nine are evidently paleotetraploid, nine others, paleohexaploids. The most frequent chromosome number in Winteraceae, $n = 43$, is evidently paleododecaploid. Of the remaining 15 families of the subclass Magnoliidae for which information is available, seven have diploid basic numbers, seven polyploid numbers, and one (Saururaceae, $x = 11$, 12?) is ambiguous.

In Hamamelididae, the only diploids are found in Betulaceae-Carpinioideae, with $x = 8$, and in Casuarinaceae, with $x = 8$, 9. Of the remaining 14 families for which information is available, 10 have evidently had a tetraploid origin, four a hexaploid origin. Urticales have evidently been derived from a common tetraploid ancestor with $n = 14$.

In Caryophyllidae, 12 of the 13 families for which sufficient information is available seem to have been derived from diploid ancestors, with Basellaceae and Caryophyllaceae doubtful in this respect. The two chromosome counts reported for Didiereaceae range from $n = 75$–100.

For most of the remaining orders, the interpretation of many of the inferred basic chromosome numbers becomes ambiguous. In a particularly frequent situation, it is difficult to determine whether a group has had $x = 7$ followed by increasing aneuploidy, or tetraploidy on this number followed by decreasing aneuploidy. Only detailed knowledge of the orders and a careful evaluation of whether their constitution is appropriate will lead to the resolution of this question. Certain groups, on the basis of present knowledge, appear to have had particularly high basic chromosome numbers: among these, in addition to Didiereaceae, might be mentioned Actinidiaceae ($x = 29, 30$); Bombacaceae ($x = 36$ and higher numbers, with doubtful reports of $n = 14$ and 28 in *Durio*); Nepenthaceae ($x = 39$); and Pandanaceae ($x = 30$). Hippocastanaceae ($x = 20$), Platanaceae ($x = 21$), Salicaceae ($x = 19$), and many other families are presumably of paleohexaploid origin. An especially interesting pattern is found in families such as Araceae, Bignoniaceae, Bromeliaceae, and Oleaceae, in which paleotetraploids and paleohexaploids, but no diploids, are known to exist at present.

Families with basic chromosome numbers of $x = 9$ are fairly unusual, and include, in addition to most of those of the subclass Caryophyllidae, Thymelaeaceae and Rutaceae (Rosidae, certainly unrelated); and Brunoniaceae and perhaps Goodeniaceae (x might $= 8$), as well as the families of Dipsacales and Asterales of the Asteridae.

The discussion to this point demonstrates the limited utility of chromosome numbers in question of the placement of particular families. With the basic number $x = 7$ running throughout the dicots, and $x = 11$–14 especially frequent derivatives, only the most unusual chromosome number will tend either to confirm or deny a particular suggestion of affinity. On the other hand, chromosome numbers and morphology have been enormously useful within families and between closely related families in suggesting relationships. In addition, more conclusive information is required concerning the original basic chromosome number of many families. A few examples will illustrate the point; others have been mentioned in the detailed review above.

For example, Fouquieriaceae ($x = 12$) are placed by Hutchinson (1959) and by Cronquist (1968) in Violales and by Takhtajan (1969) in an order segregated from this alliance, Tamaricales; but Thorne (1968), on the basis of a detailed anatomical and morphological study, placed it in Solanales. Both Solanaceae and Tamaricaceae, families that have not been thought to be directly related, have $x = 12$. Takhtajan (1969) places Loasaceae ($x = 7$) in Polemoniales, Thorne (1968) and Cronquist (1968) places it in Violales (Cistales); both orders have $x = 7$. The examples could be multiplied. On the other hand, there are examples in which cytological evidence is more helpful.

The heterogeneity of Amentiferae is accepted by a majority of contemporary students of angiosperm phylogeny. It would be expected, therefore, that chromosomal evidence might be important in corroborating this heterogeneity. A summary of the basic chromosome numbers in this group, as recognized by Melchior (1964), is presented in Table 2.

Several points can be made concerning these families from the standpoint of cytology. Melchior's (1964) grouping of Myricales and Juglandales into a single

TABLE 2. Basic chromosome numbers in Archichlamydeae, orders 1–14 (Melchior, 1964).

Taxon	$x =$	Taxon	$x =$
1. Casuarinales		9. Santalales	
Casuarinaceae	8, 9	9a. Santalineae	
2. Juglandales		Olacaceae	10, 12, 19
Myricaceae	16	Dipentodontaceae	—
Juglandaceae	16	Opiliaceae	10
3. Balanopales		Grubbiaceae	—
Balanopaceae	—	Santalaceae	6, 5
4. Leitneriales		Myzodendraceae	—
Leitneriaceae	16	9b. Loranthineae	
5. Salicales		Loranthaceae	
Salicaceae	19	Loranthoideae	12
6. Fagales		Viscoideae	14, 10–13
Betulaceae	7? (8, 14)	10. Balanophorales	
Fagaceae	13 (14?)	Balanophoraceae	18
7. Urticales		11. Medusandrales	
Rhoipteleaceae	—	Medusandraceae	—
Ulmaceae	14	12. Polygonales	
Eucommiaceae	17	Polygonaceae	10, 11, 12
Moraceae	14	13. Centrospermae	9
Urticaceae	14	14. Cactales	
8. Proteales		Cactaceae	11
Proteaceae	7		

order is supported cytologically, and so would the notion of a close relationship between Leitnerales and this group. Eucommiaceae do not fit well into Urticales on cytological grounds, and they are separated by Cronquist (1968) and as a suborder by Thorne (1968). Santalales and Balanophorales appear distinctive cytologically. Polygonaceae appear distinct from Centrospermae, but then so do Cactaceae, linked with them by the presence of betalins. Garryaceae, once placed with Amentiferae, have $x = 11$ like other Cornales, and are now referred to that order.

What this review of chromosome numbers in Amentiferae perhaps illustrates, however, is that cytology provides no compelling reasons for separating these families or for grouping them. The relationships of Casuarinaceae are obscure and are not clarified by a consideration of the distinctive base chromosome numbers, $x = 8$ and 9, in this group. They, together with Juglandales, Balanopales, Leitnerales, Fagales, and Urticales, are grouped by Cronquist (1968) in the subclass Hamamelididae, whereas only Casuarinales, Fagales, and Balanopales are included by Thorne (1968) in his superorder Hamamelidiflorae. Thorne allies Urticales with Malvales and other groups in his superorder Malviiflorae, but since Urticales, Malvales, Fagales, and the angiosperms as a whole all ultimately have a basic chromosome number of $x = 7$, no additional help is provided by cytology in making this decision. Salicales would have a distinctive basic chromosome number, $x = 19$, whether placed in Dilleniidae (Cronquist, 1968), Cistiflorae (Thorne, 1968), or left near Fagales (Melchior, 1964); however, the position accorded Salicaceae by Thorne and Cronquist does not differ in essence and

probably reflects the known facts better than the treatment of Melchior. Both Thorne (1968) and Cronquist (1968) regard Centrospermae (with Cactales and Polygonales) as an early evolutionary offshoot among the angiosperms, and their positions do not therefore differ much from that of Melchior (1964). Santalales and Balanophorales are regarded by both Thorne (1968) and Cronquist (1968) as related to Celastrales, and basic chromosome numbers of $x = 6$ and $x = 12$ are common to these groups. Whether Oleales are also related to this assemblage, as postulated by Thorne (1968), or to Asteridae (Cronquist, 1968), is open to question. Cytological evidence suggests that Celastrales, Santalales, and Rhamnales are related and derived from a common ancestor in which $x = 6$ relatively early in the history of the angiosperms; it does not support the placement of Oleaceae, with a basic chromosome number of $x = 14$ and probably ultimately $x = 7$, in a position of direct relationship to this group.

In his subclass Dilleniidae, Cronquist (1968) includes Thorne's (1968) superorder Cistiflorae in addition to his Theiflorae. Cytological evidence is inconclusive on this point; the groups are not highly distinctive and are regarded as related in both systems. Thorne's (1968) Malviiflorae includes, in addition to Urticales and Malvales, Euphorbiales, Solanales, Campanulales, and Rhamnales, all with basic chromosome numbers easily derived from $x = 7$. His superorder Santaliflorae, however, as already mentioned, includes only Santalales and Oleales. Rhamnaceae seem on cytological grounds to be allied to Celastrales, but Elaeagnaceae, allied by Thorne with Rhamnaceae, may have $x = 7$ ultimately instead of $x = 12$, and are probably better placed elsewhere. Cronquist (1968) and Takhtajan (1969) have placed them near Proteaceae, which also have $x = 7$. Oleales, also included by Thorne (1968) and Takhtajan (1969, as Celastranae) with Santaliflorae, also have $x = 7$, and are perhaps better included with Scrophulariales (Thorne's Bignoniales), following Cronquist (1968). In other words, cytological evidence suggests a modification of Thorne's Santaliflorae by the exclusion of Oleales and the addition of Rhamnaceae, Leeaceae, and Vitaceae, the latter two families assigned by Thorne (1968) to the Cornales, where they are cytologically discordant. Thorne's (1968) Santaliflorae would then be equivalent to Takhtajan's (1969) Celestranae, Takhtajan also including Oleales.

In Thorne's superorder Rutiflorae are included Rutales, Myricales, and Leitneriales. Juglandaceae (with Rhoipteleaceae) are placed in Rutales. Although the morphological and anatomical evidence for a relationship between Juglandaceae and such rutalean families as Anacardiaceae seems conclusive, cytological evidence also favors a common ancestry for the traditionally allied Juglandaceae, Myricaceae, and Leitneriaceae, all with $x = 16$. Perhaps these families, with Rhoipteleaceae, would better be treated as a second order of Rutiflorae. Cytologically they are discordant in Hamamelididae (unless directly related to *Liquidambar*), where placed by Cronquist (1968) and Takhtajan (1969), but fit very well with Rutales (Cronquist's Sapindales), where basic chromosome numbers of $x = 16$ are frequent. In Cronquist's system, they should probably constitute an order or orders following Sapindales. As stressed by Takhtajan (1969: 104–105), the very reduced flowers of plants such as *Leitneria* make their affinities very difficult to determine.

Thorne's (1968) superorder Gentianiflorae includes Bignoniales (Scrophulariales), $x = 7$, and Gentianales, with the same composition as Cronquist's group together with Rubiaceae (essentially the arrangement of Melchior, 1964). The basic chromosome number for Gentianales may be $n = 7$, but Apocynaceae and Asclepiadaceae, as well as Antoniaceae and Strychnaceae (segregates from Loganiaceae), have $x = 11$ like Rubiaceae. Cronquist's (1968) placement of Rubiaceae as a unifamilial order near Campanulales and Dipsacales is neither favored nor strongly contradicted by cytological evidence, but Thorne's treatment resembles that of Takhtajan (1969) and is perhaps more conservative.

On cytological grounds, there seems to be a relationship between a number of orders of Cronquist's (1968) Rosidae: Linales, Polygalales, and Umbellales, with $x = 6$, Myrtales perhaps with $x = 12$, Cornales with $x = 11$, and perhaps even Santalales ($x = 6$), Celastrales ($x = 12$), and Rhamnales ($x = 12$). The special relationship between Cornales and Umbellales in Cronquist's sense, implied by Thorne's grouping them into an order Cornales, is uncertain, and there seems to be some relationship between Myrtales and this group.

Cytological evidence, like the evidence from floral anatomy (Eyde, this symposium), tends to contradict a derivation of Proteaceae ($x = 7$) and Elaeagnaceae ($x = 7$) from Myrtales ($x = 12, 11$), where Thymelaeaceae ($x = 9$) are also apparently discordant. All three families might be accommodated more easily earlier in the rosid line.

These and other questions must, however, be decided in the light of all the evidence, and what is feasible cytologically might be contradicted on other grounds. Nevertheless, cytology does have its contribution to make to our understanding the bases of angiosperm phylogeny. We are now able to improve on the pioneering efforts of Darlington & Mather (1949), especially in view of the fact that information is available for three times as many genera—perhaps 40% of the total. When more of the gaps have been filled, and especially when we have the results of comprehensive investigations of many families in which chromosomal evidence is combined with all other available evidence to produce a reasonable hypothesis concerning original basic chromosome number, it will be possible to advance our deductions about the patterns of cytological evolution in the angiosperms still farther.

THE PATTERN IN LILIOPSIDA (MONOCOTYLEDONEAE)

As should be evident from the summary presented earlier, much less can be said about the evolution of chromosome numbers in monocots than in dicots. Certainly $x = 7$, the original basic chromosome number of angiosperms, is much in evidence in the monocots as well as in the dicots, and could easily be the original basic chromosome number for Alismatales, Hydrocharitales ($x = 6$ is also frequent), Restionales, Zingiberales, and Arales on the basis of present evidence. For the large families Commelinaceae, Liliaceae sensu lato, and Orchidaceae, although there is much information about chromosomes, it would clearly be premature to advance a hypothesis concerning the original basic number. High basic chromosome numbers are characteristic of Flagellariaceae, $x = 19$; Bromeliaceae, $x = 17, 25$; Arecaceae, $x = 18$; and Pandanaceae, $x = 30$–32. The

first three of these are at least paleotraploid, the last at least paleohexaploid. The systems for the monocots of Hutchinson (1959), Melchior (1964), Thorne (1968), Cronquist (1968), and Takhtajan (1969) are similar enough that there are relatively few problems of placement to discuss in the light of cytological evidence. The vexed subject of family limits in the Liliales is one in which cytological information is not helpful, although there is a great cytological diversity which will continue to be helpful in understanding the relationships of particular species and genera.

EVOLUTIONARY TRENDS

Even though evolutionary changes in chromosome number and morphology have been frequent and may seem to have given rise to a bewildering diversity of situations (Stebbins, 1971), some generalities can be derived concerning evolutionary trends. Among them are the following.

The original basic chromosome number in angiosperms seems clearly to have been $x = 7$, characteristic of all major groups of both dicots and monocots except Caryophyllidae, with $x = 9$. This implies clearly that most progressive evolution has been at the diploid level (Stebbins, 1950, 1967, 1970), even though polyploidy has been very important in the evolution of families and even orders. The subclasses devised by Armen Takhtajan more than a decade ago have remained very useful conceptually, but the distinctions between Dilleniidae and Rosidae seem to be more and more dubious (Eyde, this symposium), and Asteridae may be diphyletic (Hickey & Wolfe, this symposium). When these lines are better understood, so will be the pattern of chromosomal evolution they have undergone.

It is of interest to compare the original basic chromosome number of angiosperms with those found in various groups of gymnosperms. *Ephedra* has $x = 7$ and *Welwitschia*, $x = 21$, but there are a variety of reasons for doubting that they had a common ancestor with angiosperms in which $n = 7$. *Gnetum* has $x = 12$. In the Coniferophyta, *Ginkgo* has $n = 12$, as do a variety of other genera, with $n = 11$ also very frequent. Noteworthy are Araucariaceae and *Pseudotsuga* (Pinaceae) with $n = 13$, *Sciadopitys* (Taxodiaceae) with $n = 10$, and a great variety of chromosome numbers in Podocarpaceae. In Cycadophyta, $n = 8$, 9, and 11 are represented (Marchant, 1968).

The high incidence of polyploidy in Annoniflorae and Hamamelidiflorae strongly suggests that the ancestors of many of the surviving families were polyploids that invaded newly opened habitats in mid-Cretaceous time (Stebbins, 1950). The opening of these habitats and the success of the early angiosperms might well be correlated with climatic changes accompanying the opening of the Indian Ocean 150 million years ago, and especially with the separation of Africa from South America which began 125–130 million years ago (summary in Raven & Axelrod, 1974). On the other hand, polyploids are not so well represented among the basal orders of Cronquist's Dilleniidae, including families such as Dipterocarpaceae which are typical of the tropical lowland rain forest. As stressed by Takhtajan (1969), many of the primitive members of Annoniflorae and Hamamelidiflorae occur in subtropical mountains with a very equitable climate, and not in the tropical lowland forest. This suggests that the "newly opened

habitats" mentioned above may not have been the tropical lowland forest, but rather the relatively temperate mountains in or near the tropics. An expansion of such habitats is not known to have occurred in the mid-Cretaceous. It may be that polyploids have simply accumulated in the equitable tropical mountains and islands as conservative offshoots of the mainstream of angiosperm evolution, with polyploidy itself playing a retarding role on progressive evolution.

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THE BASES OF ANGIOSPERM PHYLOGENY: CHEMOTAXONOMY[1,2]

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Abstract

The use of the distribution patterns of plant natural products—alkaloids, terpenes, phenolics, etc.—is well established as a major tool for investigating population structures, species, and phyletic relationships of genera. Here, it is suggested that the distribution patterns of biogenetically closely related substances should be of considerable value for deducing evolutionary relationships at higher taxonomic levels. Approximately 540 plant taxa (cultivars through orders) have been included in approximately 150 systematic serological publications in the last 25 years. Research has demonstrated that extracts of seeds, pollen, leaves, tubers, and spores of vascular plants can be used if the required extraction procedures are followed. Both quantitative and qualitative immunological techniques have provided complementary data which have proven to be provocative and valuable in the classification of higher plants. The examples presented clearly indicate serology has contributed chemical data which can be—and have been—used with other data to aid in producing systems of classification such as those of Cronquist and Takhtajan. The phylogenetic relationships among 15 species belonging to 12 families of vascular plants based on a comparison of cytochrome *c* amino acid sequences agree in general outline with morphologically based phylogenetic diagrams. Amino acid sequence data on homologous plant proteins are in too limited a supply to permit other than very preliminary phylogenetic comparisons. Acquisition of more data will require considerable time and work before an impact will be realized. Published protein sequence data have not revolutionized presently accepted phylogenetic diagrams, and it is too soon to hint at the ultimate contribution of sequence data to phylogenetic schemes. The technique of nucleic acid hybridization is, in principle, applicable to chemotaxonomy at all taxonomic levels since it involves the fundamental hereditary material deoxyribonucleic acid (DNA) and its transcribed copy, ribonucleic acid (RNA). In contrast to the relative ease with which meaningful plant natural products distribution patterns are determined, are the difficulties and patience required to carry out nucleic acid hybridization experiments and to interpret the results from them. Thus, it is not surprising that few nucleic acid hybridization data for higher plants are available to meaningfully influence the interpretations of Cronquist and Takhtajan for the evolution of the angiosperms; nevertheless, the method inherently has great potential.

General Introduction

With the development of plant natural products chemistry, which deals with a myriad of alkaloids, phenolics, mustard oils, terpenoids, etc., botanists and chemists have revealed that it is possible to employ chemical constituents to help characterize, classify, and describe taxa. Attempts to correlate morphological and chemical characteristics are very old. Greene (1909) indicated that the most remote and primitive of botanical writers, of whatever country, found a botanical

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vocabulary in the colloquial speech. The reason for this was the many uses of local plants. These uses resulted from the plants' distinctive chemistry, as reflected in color, esculence, flavor, odor, or toxicity.

Petiver (1699) published about the correlations between medicinal (chemical) properties and certain morphological groupings. He used "Herbae Umbelliferae" together with the Labiatae and Cruciferae to illustrate the hypothesis that morphologically similar plants produce constituents (chemicals) with similar therapeutical effects. Hoffmann (1846) in his treatment of families of flowering plants described the chemical characteristics of each of them. He believed that phytochemistry offered the opportunity to check proposed classifications based solely on morphological characteristics. Greshoff (1893) stated several basic tenets. One stated that biochemists and phytochemists had to investigate evolutionary tendencies of metabolic pathways and groups of chemically related plant constituents much more thoroughly before they would achieve an understanding of evolution comparable to that of morphologists. McNair's (1965) book, which is a reprinting of his published papers, considered taxonomy in relation to oils, fats, waxes, oil and starch in seeds, and alkaloids. McNair's 1935 reprinted paper "Angiosperm Phylogeny on a Chemical Basis" included in his book has a "ring" very similar to the present symposium. Gibbs (1974) published a book (encyclopedic) containing four volumes in which he reported chemical information from a vast amount of literature and chemical tests on numerous flowering plants.

Although the concept of employing chemical data in systematic investigations is an old one, a genuine and intensified endeavor to understand possible correlations between plant constituents and classification has been relatively recent. Chemical characteristics were neglected for a long time because information in most plant groups was too scanty and scattered for any individual group. Interest in this type of research has increased as more data have been obtained from biochemical, immunochemical, and organic chemical research. The development of relatively quick and simple analytical techniques has hastened the "coming of age" of chemotaxonomy.

The "present age" of chemosystematics or chemotaxonomy commenced in the mid 1950's. The oldest of the "present age" plant chemotaxonomic approaches is serotaxonomy and the youngest is amino acid sequencing.

Three books (Alston & Turner, 1963; Swain, 1963; Leone, 1964) provided general information and/or reviews about the early chemotaxonomic and serotaxonomic research. Since that time, numerous comprehensive chemotaxonomic reports have been published in journals, symposia, reviews, and books which clearly indicate the mounting interest in this diversified field of research (Bendz & Santesson, 1974; Boulter et al., 1972; Boulter, 1973; Fairbrothers, 1968, 1975; Harborne, 1967, 1968, 1970; Harborne & Swain, 1969; Harborne et al., 1971; Hawkes, 1968; Hegnauer, 1962–1973; Heywood, 1971; Hunziker, 1969; Kubitzki, 1969, 1972; Mabry et al., 1968; Runeckles & Mabry, 1973; Runeckles & Tso, 1972; Runeckles & Watkins, 1972; Seikel and Runeckles, 1969; Steelink & Runeckles, 1970; Swain, 1973; Turner, 1969; Vaughan, 1968).

Most chemical approaches to systematic problems can be classified according

to the kind of molecules investigated. If the compounds are of relatively low molecular weight (free amino acids, alkaloids, phenolics, terpenes, etc.) they are designated micromolecules. If the compounds are of high molecular weight and polymeric (carbohydrates, DNA or RNA, and proteins) they are designated macromolecules.

Micromolecules—Plant Natural Products

Since the first attempt to place into any kind of perspective the potential of chemical characters for systematics—Alston & Turner's (1963) *Biochemical Systematics*—we have witnessed a deluge of chemotaxonomic reports, reviews, volumes, and symposia; much of these data have been painstakingly assembled by Hegnauer (1962–1973) and co-workers into six volumes. This burst of activity resulted in part because some sort of structurally precise chemical information can be readily obtained for every plant available for investigation. And the complex chemical structures often represent hundreds of genes.

However, despite the wealth of chemical information, only a few systematically meaningful interpretations have emerged. Nevertheless, the future for gaining new insights into angiosperm phylogeny using micromolecular data is bright as more and more future Cronquists and Takhtajans become trained in plant chemistry.

Before discussing the extent to which natural products are important for phylogeny at the higher taxonomic categories of angiosperms and the implications of the distributions of these compounds with respect to the Takhtajan and Cronquist systems, certain definitions and general remarks regarding such plant constituents are in order. The expression "plant natural products" is used here to denote the million or so alkaloids, terpenes, phenolics, quinones, etc. which have restricted distributions in plants. It is the "restricted distribution" phenomenon which permits these substances of low molecular weights, usually less than 1000, to be employed as phyletic markers.

Each plant species probably produces from about fifty to several hundred natural products for a variety of functions, including metabolism, defense, structure, and energy and material storage. For the most part, these functions have determined which compounds and which structural features within classes of compounds have been either conserved or modified by selection; however, some modifications of the natural products chemistry may have resulted secondarily as selection operated upon the early stages of pathways leading to the natural products. In any case, it is not uncommon to find that a high percentage of a plant's chemistry, sometimes more than 80–90%, has been conserved such that it occurs in a group of closely related species. Although for higher taxonomic categories the percentages become less, it is frequently possible at the level of tribe, family, and order to recognize biogenetically related compounds which reflect the plant's evolutionary history. It is these latter types of chemical patterns, which involve the distribution of biogenetically homogeneous classes of natural products, that form the basis of the present discussion.

It is not feasible to indicate taxonomically diagnostic classes of natural products for all orders and families; instead a few selected examples are evaluated with

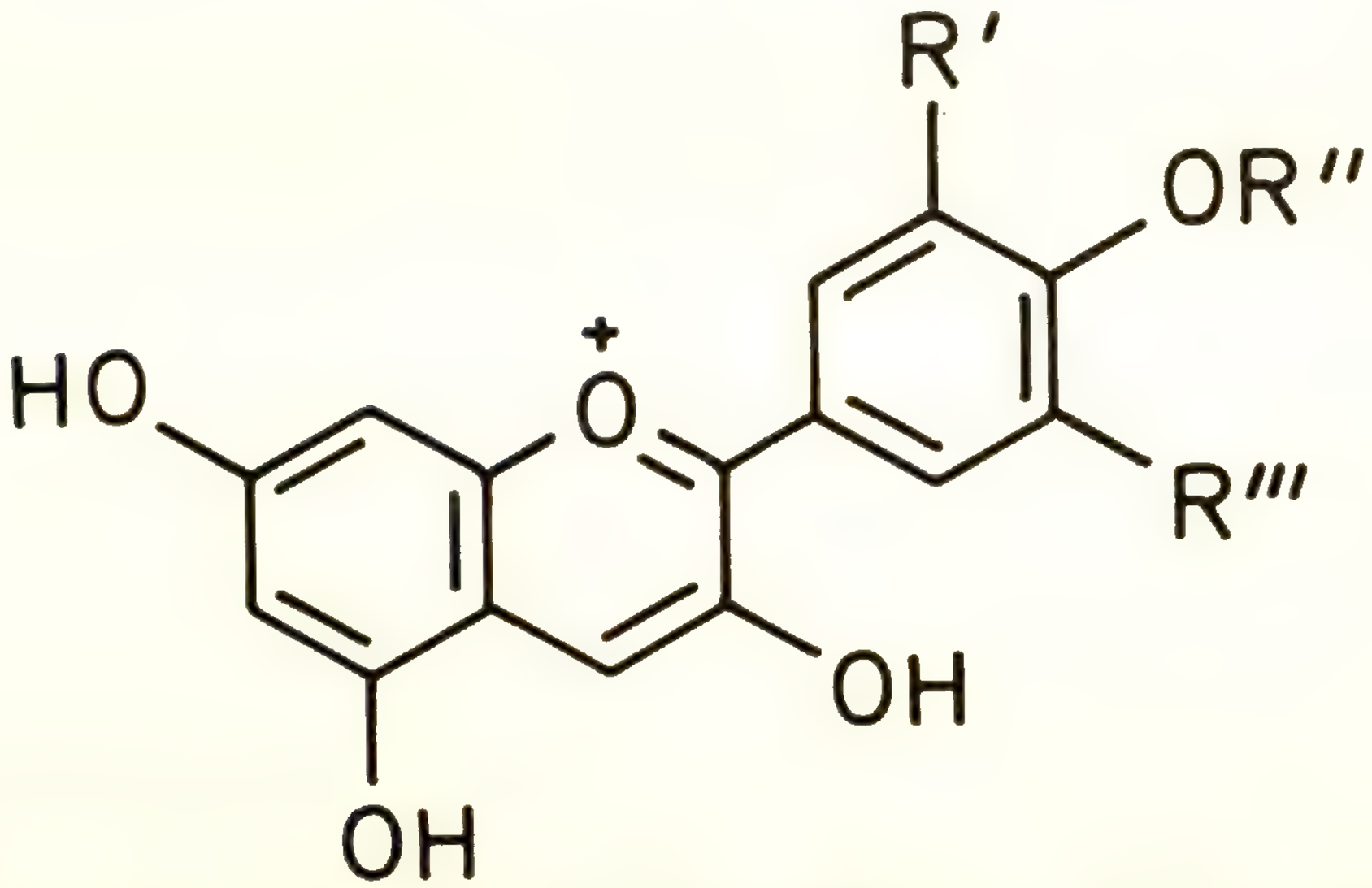


FIGURE 1. Anthocyanidins contained as the aglycone in anthocyanins. Pelargonidin: $R'^{-'''} = H$; cyanidin: $R''^{-'''} = H$, $R' = OH$; peonidin: $R''^{-'''} = H$, $R' = OCH_3$; delphinidin: $R'' = H$, $R'^{-'''} = OH$; petunidin: $R'' = H$, $R''' = OH$, $R' = OCH_3$; malvidin: $R'' = H$, $R'^{-'''} = OCH_3$.

respect to the interpretations of Cronquist (1968) and Takhtajan (1969) for the taxa involved.

It should be emphasized that the application of the distribution of a particular class of natural products for phylogeny assumes that the same or similar structures are derived by evolutionally related sets of enzymes. Although this hypothesis is almost certainly true in most instances, especially at the generic level, it should be recognized that the independent origin of some substances apparently does occasionally occur in unrelated taxa.

PIGMENTS

Anthocyanins (anthocyanidin glycosides) are widely distributed in angiosperms and most higher plants (except for those producing betalains) contain as the aglycone one or more of six anthocyanidins: pelargonidin, cyanidin, peonidin, delphinidin, petunidin and malvidin (Fig. 1).

Thus, because most plants contain anthocyanins with the same or similar anthocyanidins and glycosyl moieties, these substances are of little value for phylogenetic purposes. Even the odd distribution pattern such as the scarcity of pelargonidin in Australian plants has been attributed to the low frequence of bird pollinating mechanisms for the Australian flora rather than to phylogeny (Harborne, 1967). Anthocyanidins other than the six common ones are very rare and few in number, being found regularly in only three families, Primulaceae, Plumbaginaceae, and Gesneriaceae, all of which are treated as being phyletically unrelated by both Cronquist (1968) and Takhtajan (1969).

In contrast to the taxonomic insignificance of the distribution of the anthocyanidins, the occurrence of the red-violet and yellow betalains in several evolutionally-related families (Table 1) of what some workers refer to as the order Centrospermae (see, for example, Mabry et al., 1963) represents one of the

TABLE 1. Betalain-producing families of the order Centrospermae (Mabry, et al., 1963) or Caryophyllales (Cronquist, 1968; Takhtajan, 1969).

Aizoaceae	Didiereaceae
Amaranthaceae	Nyctaginaceae
Basellaceae	Phytolaccaceae
Cactaceae	Portulacaceae
Chenopodiaceae	

classic examples of the way a group of low molecular weight substances have been conserved at higher taxonomic categories, and thus can be employed as genetic markers at these levels (Mabry et al., 1972, and references therein).

The betalain pathway has provided a group of evolutionally-related plants (see also NUCLEIC ACID HYBRIDIZATIONS below) with substances which replace the red and yellow anthocyanin pigments common to most angiosperms. As far as is known, the two classes of pigments, anthocyanins and betalains, never occur together in the same plant or even separately in members of the same family (Kimler et al., 1970). Comparison of wavelengths of the absorption maxima for some of these pigments indicates the importance of the chromophoric group, presumably to attract pollinators (Fig. 2); nevertheless the high concentration of betalains in the stems and leaves of the plants which produce them suggest that these compounds, like many natural products, are polyfunctional.

Unlike Mabry et al. (1963), both Takhtajan and Cronquist have included anthocyanin-producing families in the same order with the betalain-producing families. However, both Takhtajan and Cronquist, unlike most earlier systematists, did include all betalain-producing families in their order Caryophyllales. In this connection, the presence of betalains in the Cactaceae and Didiereaceae was probably a decisive factor in placing these families in this order. Cronquist aligns only two anthocyanin-producing families, the Molluginaceae and the Caryophyllaceae, in his Caryophyllales while Takhtajan also includes the Bataceae, which apparently does not produce either type of pigment (Mabry & Turner, 1964). Support for the relatively close relationship of the anthocyanin-producing Molluginaceae and Caryophyllaceae with those betalain-producing families is available from other sources, including DNA-RNA studies (for the Caryophyllaceae only; see NUCLEIC ACID HYBRIDIZATIONS below) and ultrastructural research on sieve-element plastids. Sieve-element plastids of the betalain-producing families are characterized by ring like inclusions composed of proteinaceous filaments (Behnke & Turner, 1971; Behnke, 1972, this symposium). These structures have not been observed in most other dicot families (most sieve-element plastids in dicots contain starch but no filaments). Fifty-five species belonging to the following 12 families were found to contain these unique inclusions: Phytolaccaceae, Nyctaginaceae, Didiereaceae, Amaranthaceae, Chenopodiaceae, Aizoaceae, Molluginaceae, Cactaceae, Portulacaceae, Basellaceae, Caryophyllaceae, and Dysphaniaceae (this latter taxon has just been investigated for its pigments and found to contain betalains; Mabry & co-workers, unpublished).

It is also interesting that the Polygonaceae (anthocyanin-containing)—which is treated as an order closely related to the Caryophyllales by both Cronquist

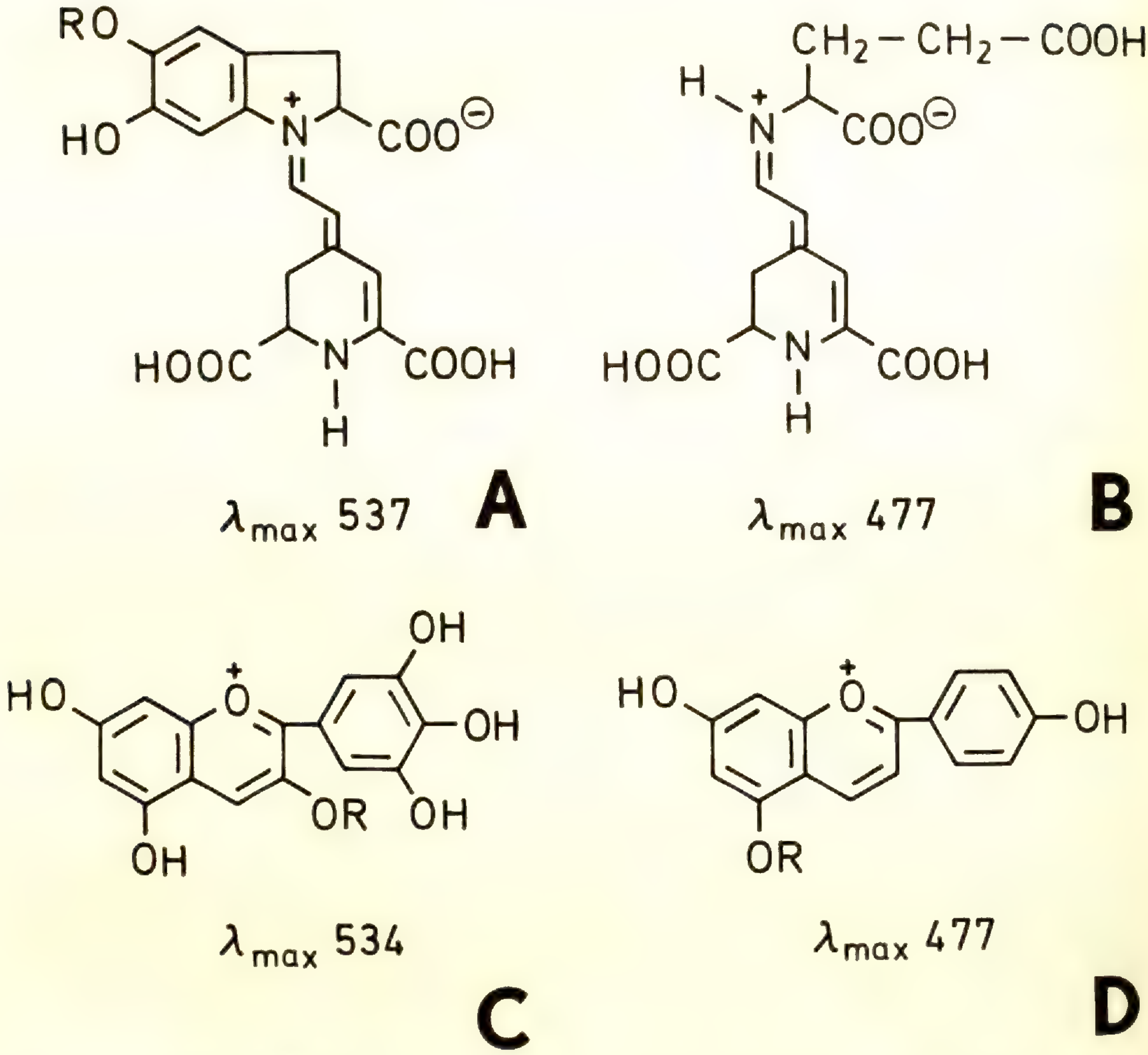


FIGURE 2. The visible absorption maxima of typical red (A) and yellow (B) betalains, which are found in nine phyletically-related plant families, are similar to those for some red (C) and yellow (D) anthocyanins, a class of pigments which occur in most flowering plant families other than those producing betalains.

and Takhtajan—as well as the Bataceae, did not contain the proteinaceous inclusions in their sieve-element plastids. As already pointed out, Takhtajan includes the Bataceae in his order Caryophyllales; however DNA-RNA studies (see below) as well as the ultrastructural data would suggest that this family is distinct from those which produce betalains (see also section GLUCOSINOLATES below). Cronquist placed the Bataceae in an order directly following his Caryophyllales but noted that it "may or may not be closely allied to (them)." The presence of anthocyanins and the absence of betalains in the Illecebraceae (see Mabry et al., 1963), treated by both Takhtajan and Cronquist as in or near the Caryophyllaceae, would suggest that they might be aligned with the Caryophyllaceae, close to but separate from the order containing the betalain families.

Among the taxa which have been traditionally treated as related to the betalain families is the Theligonaceae (Cynocrambaceae) which Cronquist and Takhtajan exclude from their Caryophyllales; Takhtajan erected an order Theligonales near

TABLE 2. Centrospermae-like taxa whose pigment content is unknown.[a]

Family	Disposition with respect to their order Caryophyllales	
	Cronquist	Takhtajan
Achatocarpaceae	Included in Phytolaccaceae	Included in Phytolaccaceae
Gyrostemonaceae	Included in Phytolaccaceae	Included in Phytolaccaceae
Barbeuiaceae	Included in Phytolaccaceae	Included in Phytolaccaceae
Sphenocleaceae	Excluded	Excluded
Hectorellaceae	Not treated	Included as a distinct family

[a] Interested collaborators are asked to send 1 gram of air-dried red-pigmented parts (flowers, leaves, or stems) of members of any of these taxa to T. J. Mabry for chemical analysis.

the Caryophyllales for this single family, whereas Cronquist placed it in the order Haloragales. More recently, Wunderlich (1971), on the basis of anatomical, morphological, and embryological evidence, placed *Theligonum* firmly in the family Rubiaceae. Strong support for this latter decision is provided by Kooiman's (1971) recent discovery that species of *Theligonum* contain terpene-derived iridoid compounds which are typical of members of the Rubiales (see Figure 10), but are not reported from the Caryophyllales. In addition, *Theligonum* does not have the proteinaceous sieve-tube plastids typical of members of the Caryophyllales (Behnke, 1972). Recently, Mabry et al. (1975) detected anthocyanins in *Theligonum cynocrambe* supporting the exclusion of *Theligonum* from the order Centrospermae.

The recent report (Hunziker et al., 1974) of betalains and P-type sieve-element plastids in *Halophytum*, a genus which has been treated as a member of the Chenopodiaceae or as a distinct family, confirms the alignment of the genus to the Centrospermae. Similarly, the discovery of betalains and P-type sieve-element plastids in *Petiveris* and *Adgestis* (Phytolaccaceae; Behnke et al., 1974) and betalains in *Giskia* (Mabry & co-workers, unpublished; not analyzed yet for sieve-element plastids) supports the assignment of these genera to the Centrospermae.

The pigments of the taxa listed in Table 2 remain to be determined. These taxa have been placed at one time or another in or near those taxa which produce betalains.

GLUCOSINOLATES (MUSTARD OIL GLUCOSIDES)

The glucosinolates are widely distributed in the families which both Cronquist (1968) and Takhtajan (1969) place in their order Capparales (Table 3). In erecting the order Capparales, Cronquist noted that "nearly all of the Cruciferae and many of the Capparaceae have specialized myrosin cells, which are chiefly though not entirely restricted to this order. . . . Myrosin is an enzyme involved in the formation of mustard oil" [from glucosinolates] (Figs. 3–5). Although there are a few reports of glucosinolates occurring outside the order Capparales, the widespread distribution of them in the five families in the first column of Table 3 supports the similar interpretations of both Cronquist and Takhtajan for this order. The partly discontinuous occurrence of glucosinolates in species of the Euphorbiaceae, Caricaceae, Gyrostemonaceae, Salvadoraceae, Limnanthaceae, and Tropaeolaceae suggest an independent origin of these substances in these taxa; it is of

TABLE 3. Order Capparales and the distribution of glucosinolates.

Cronquist	Takhtajan	Glucosinolates[a]
Capparaceae (including Koeberliniaceae, Pentadiplandraceae)	Capparaceae (including Cleomaceae, *Oceanopapaver*)	Present; *Oceanopapaver* not investigated
	Koeberliniaceae (including Canotiaceae)	Not detected in *Koeberlinia*
	Pentadiplandraceae	Not investigated
Cruciferae	Brassicaceae (Cruciferae)	Present
Moringaceae	Moringaceae	Present
Resedaceae	Resedaceae	Present
Tovariaceae	Tovariaceae	Present
	Emblingiaceae	Not investigated

[a] Distribution according to Ettlinger & Kjaer (1968) and Kjaer (private communication, 1973); see also Bataceae (in text).

interest, however, that the latter two glucosinolate-producing families are considered to be related and are placed together by both Cronquist and Takhtajan in the order Geraniales.

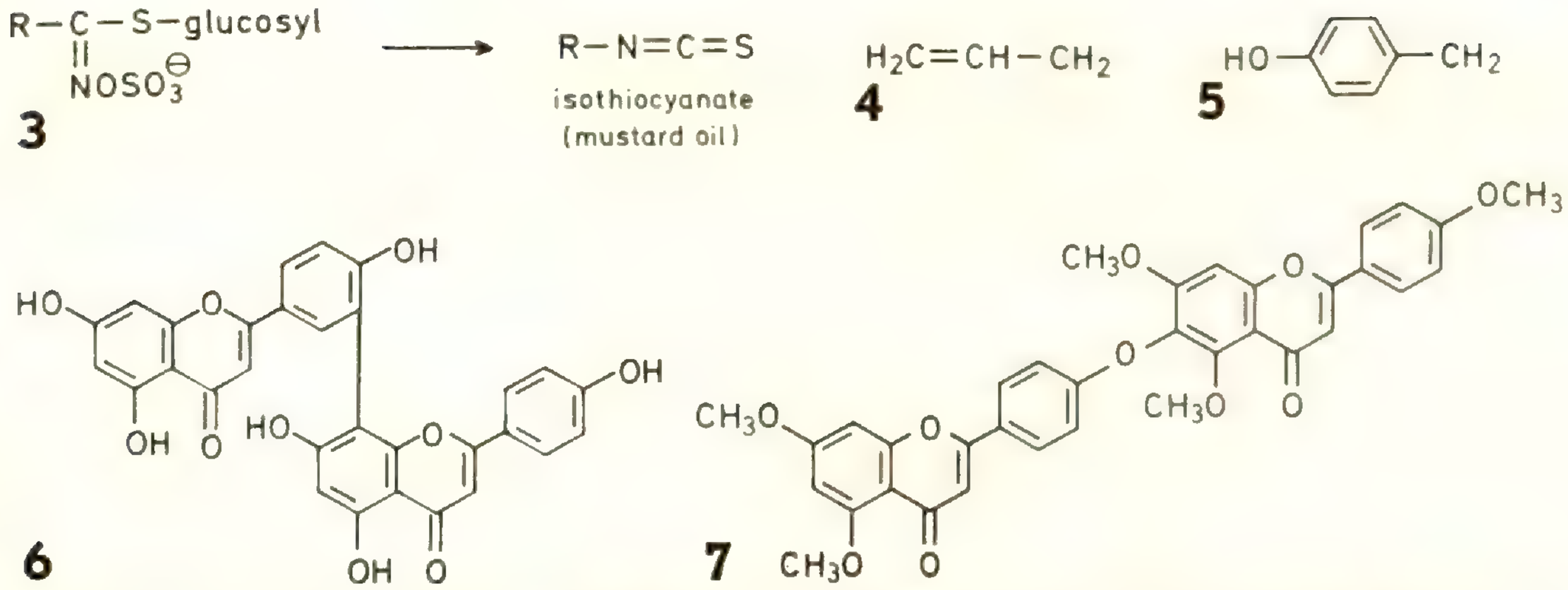
Especially interesting in relation to what has been said regarding the phyletic position of the Bataceae is the recent discovery of myrosin in this family (Schraudolf et al., 1972). But it should be noted that the Gyrostemonaceae (placed by both Cronquist and Takhtajan in the Caryophyllales) also contains myrosin, and until the pigments[6] and sieve-element plastids of this critical family are resolved it would seem premature to give undue weight to the myrosin, in spite of the morphological data which also suggests a relationship of the Bataceae with the Capparales (Eckhardt, 1959).

PHENOLICS

Phenolics in higher plants are derived almost without exception by two biogenetic pathways, the shikimate and acetate routes. Moreover, one or more classes of phenolics have been found in every plant family examined and certain structural types usually suggest evolutionary relationships at various taxonomic levels. The significance of the distribution of a few phenolics as they bear upon the views of Cronquist and Takhtajan are discussed.

Biflavonoids.—Biflavonoids, which contain two flavonoid aglycones linked by a carbon-carbon bond as in amentoflavone, or an oxygen atom as in hinokiflavone permethyl ether (Figs. 6–7), are considered to be among the more primitive phenolic substances elaborated by plants since they are reported from most gymnosperm families and from the pteridophytes. In contrast, only four mostly woody genera all from different families of angiosperms are currently known to

[6] According to B. L. Turner, personal communication, in the living state *Gyrostemon* has a very distinctive reddish-brown pigment; as yet this has not been investigated.



FIGURES 3–7. Glucosinolates and biflavonoids.—3. Glucosinolates (mustard oil glucosides), which are widely distributed in the order Capparales, are readily converted by acid or an appropriate enzyme into isothiocyanates. R can be a variety of aliphatic or aryl groups including, notably, the groups shown in Figs. 4–5.—4. Propene.—5. 4-hydroxy toluene.—6–N. Biflavonoids, which contain two monomer flavonoid aglycone skeletons linked by either a carbon-carbon bond or an oxygen atom, are considered to be primitive phenolics. 6. Amentoflavone.—7. Hinokiflavone permethyl ether.

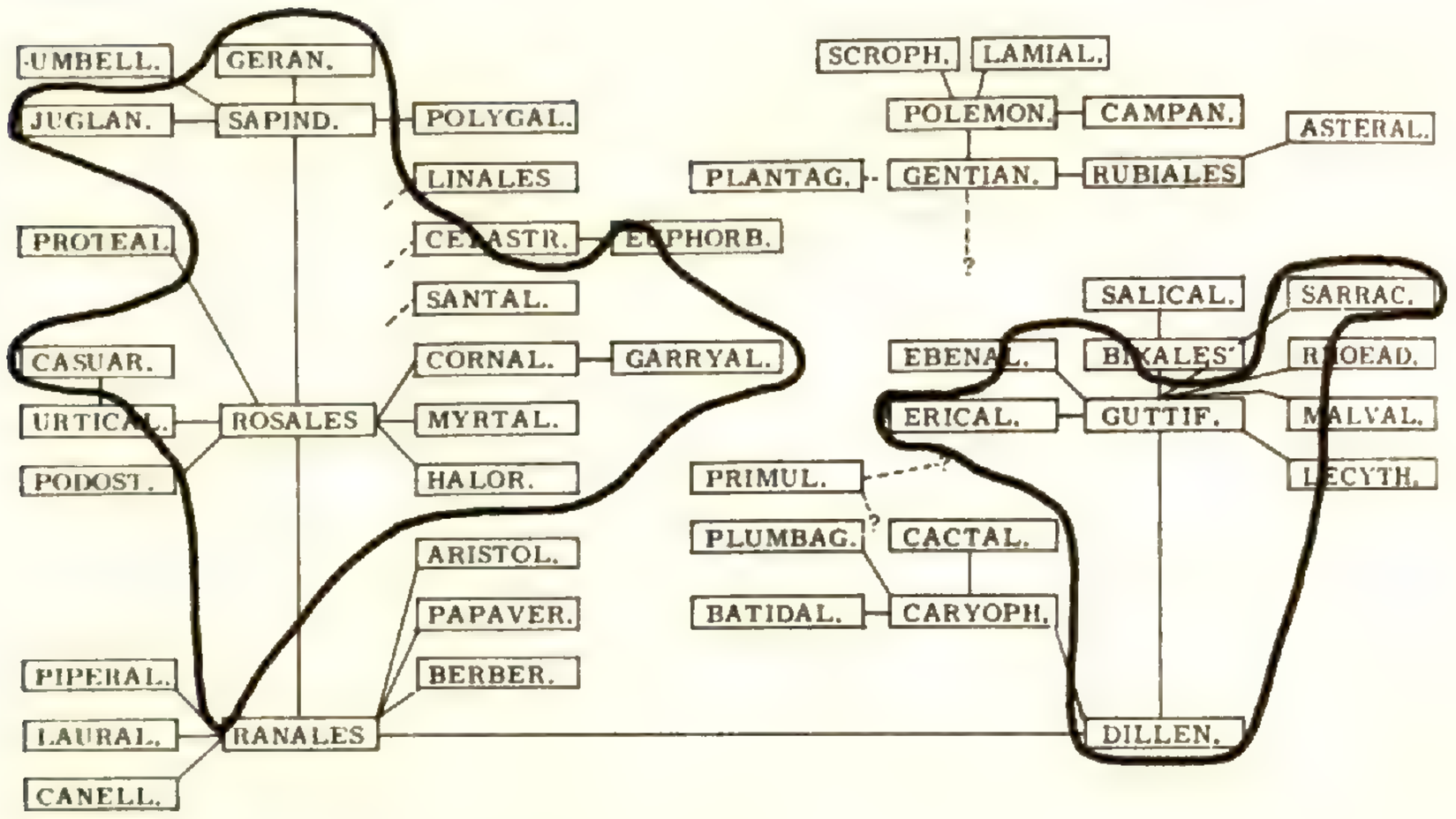
contain biflavonoids. These include *Viburnum* (Caprifoliaceae; Hörhammer et al., 1965; Glennie, 1969), *Garcinia* (Guttiferae; Herbin et al., 1970; and others) and *Hevea* (Euphorbiaceae; Madhav, 1969). However, the most interesting reports of biflavonoids in the angiosperms are those for the Casuarinaceae, a family which has been considered by at least a few previous workers (e.g. Engler and Wettstein) to be among the more primitive angiosperms. The presence of biflavonoids in *Casuarina* (see Harborne, 1967) supports these earlier views rather than those of Cronquist and Takhtajan, both of whom consider *Casuarina* to be a reduced rather than a primitive type. However, Hegnauer has privately mentioned that the polyphenols (e.g., ellagic acid) of *Casuarina* point to the Hamamelidae rather than to gymnosperms.

Vic-Trihydroxyphenolics and Leucoanthocyanidins.—The presence or absence of such phenolics as the widespread flavonols kaempferol and quercetin and their derivatives is of little use in relating plant families. On the other hand, Bate-Smith (1962, 1966, 1969) as well as others have suggested that the presence or absence of phenolics which contain vic-trihydroxy systems and leucoanthocyanidins is highly significant and that the presence of either or both is indicative of primitiveness.[7]

In terms of the origin of the monocots, it is interesting to note that Bate-Smith (1969, 1972) emphasized that "the flavonoid patterns found in monocotyledons and dicotyledons do not differ in any essential respect, nor, with one conspicuous exception, do those of the hydroxy and methoxy [phenolic] acids. . . . The exception is ellagic acid, which has never so far been found in the monocotyledons."[8] The absence of ellagic acid in the monocots and its presence in the

[7] It should be noted that the presence of leucoanthocyanidins can also be correlated to some extent with woodiness.

[8] It may, however, be significant that there are relatively few woody monocotyledons (see footnote 7 above).



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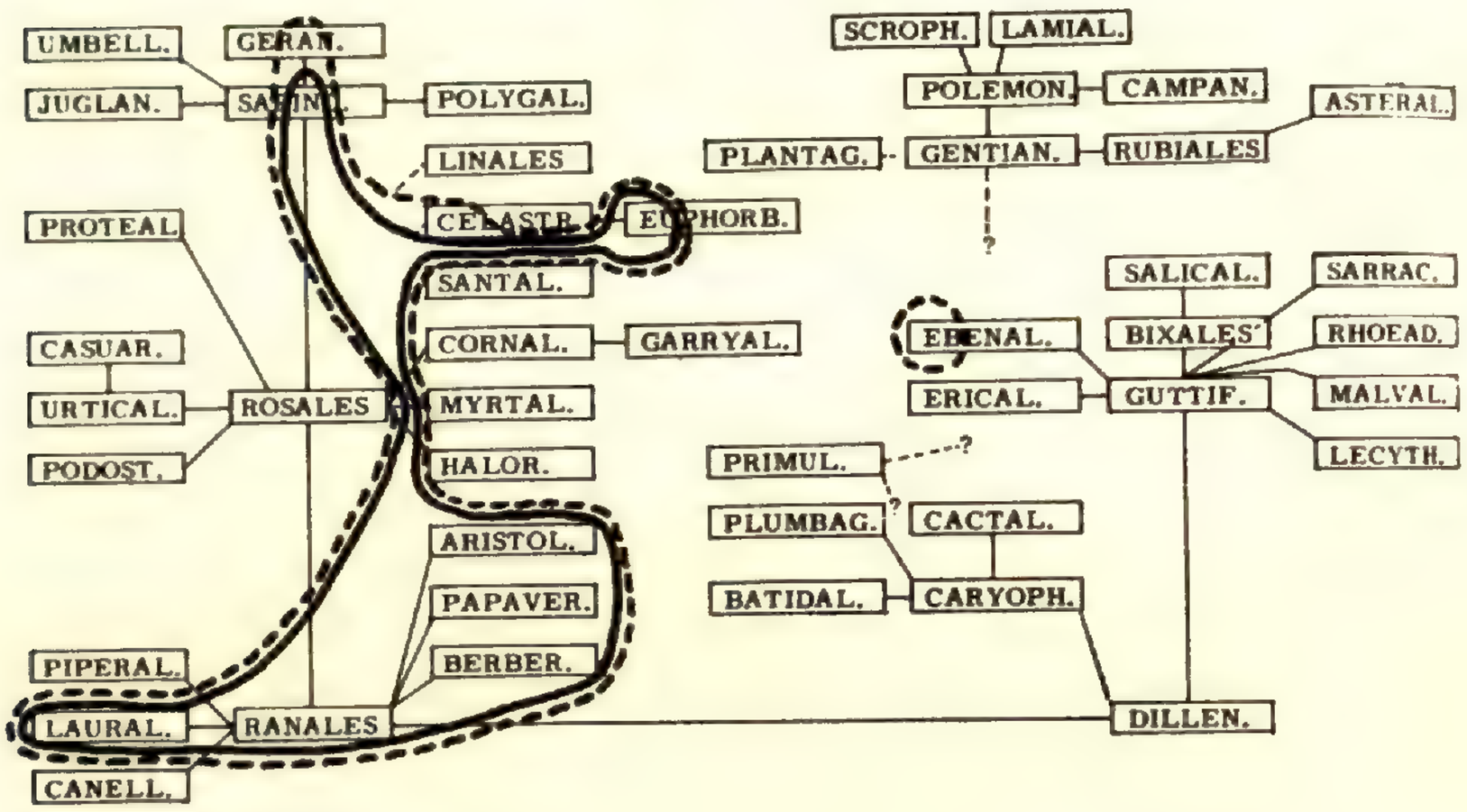
ellagic acid



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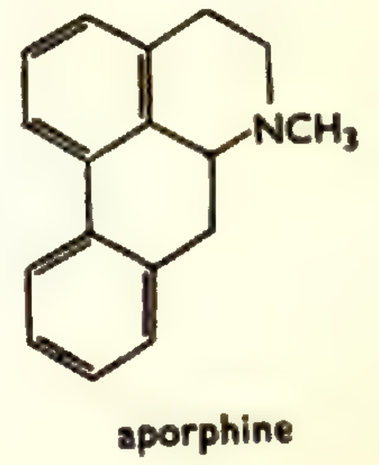
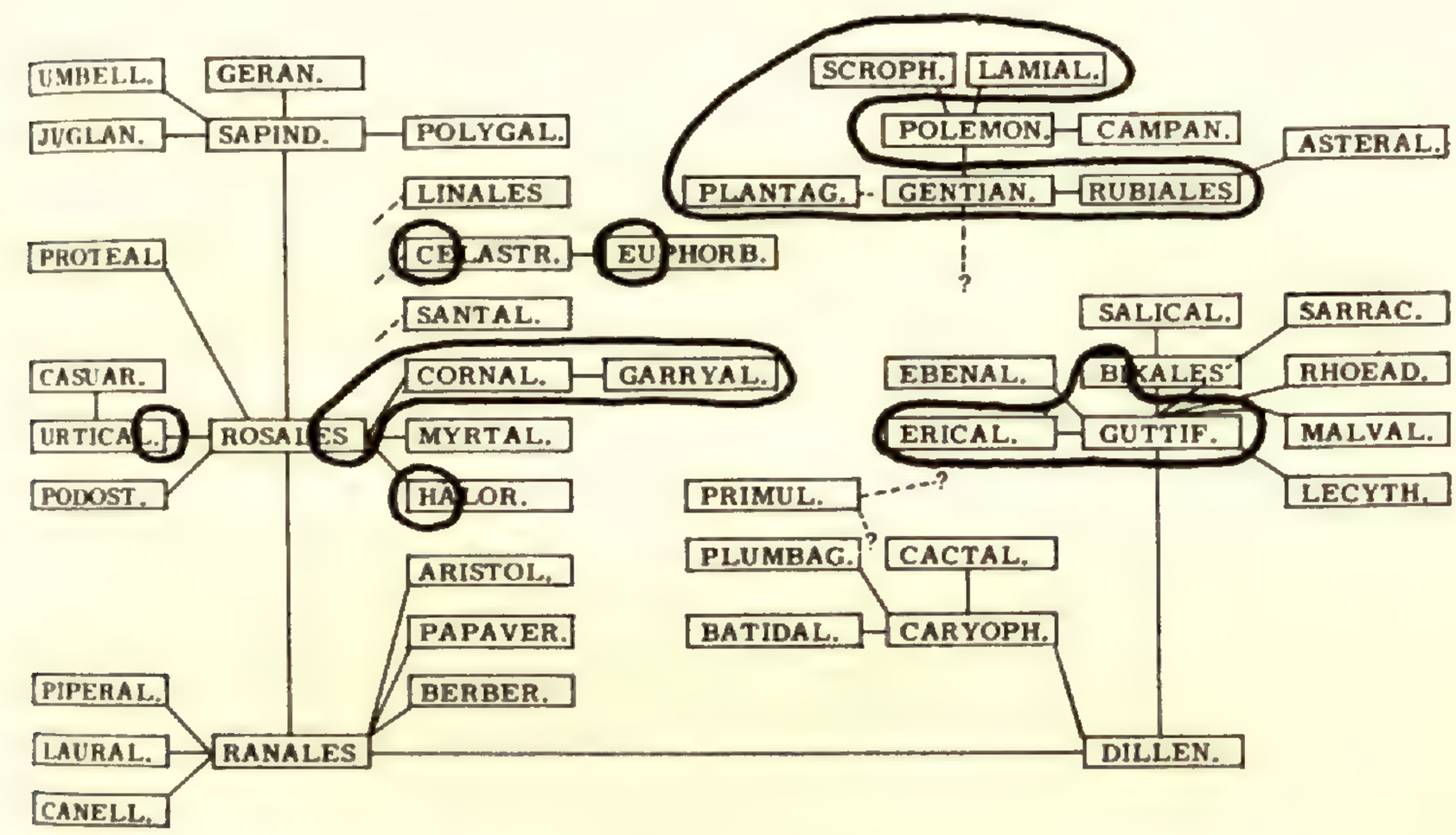


aporphine



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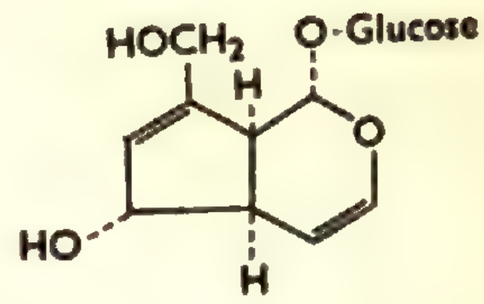

aucubin

FIGURES 8–10. The distribution of three different compounds in dicotyledons (adapted from Kubitzki, 1969).—8. Distribution of ellagic acid, which contains the elements of a vic-trihydroxyphenolic system. The presence of ellagic acid, which is not known from the monocots, is considered to be indicative of primitiveness (see Bate-Smith, 1962, 1966, 1969;

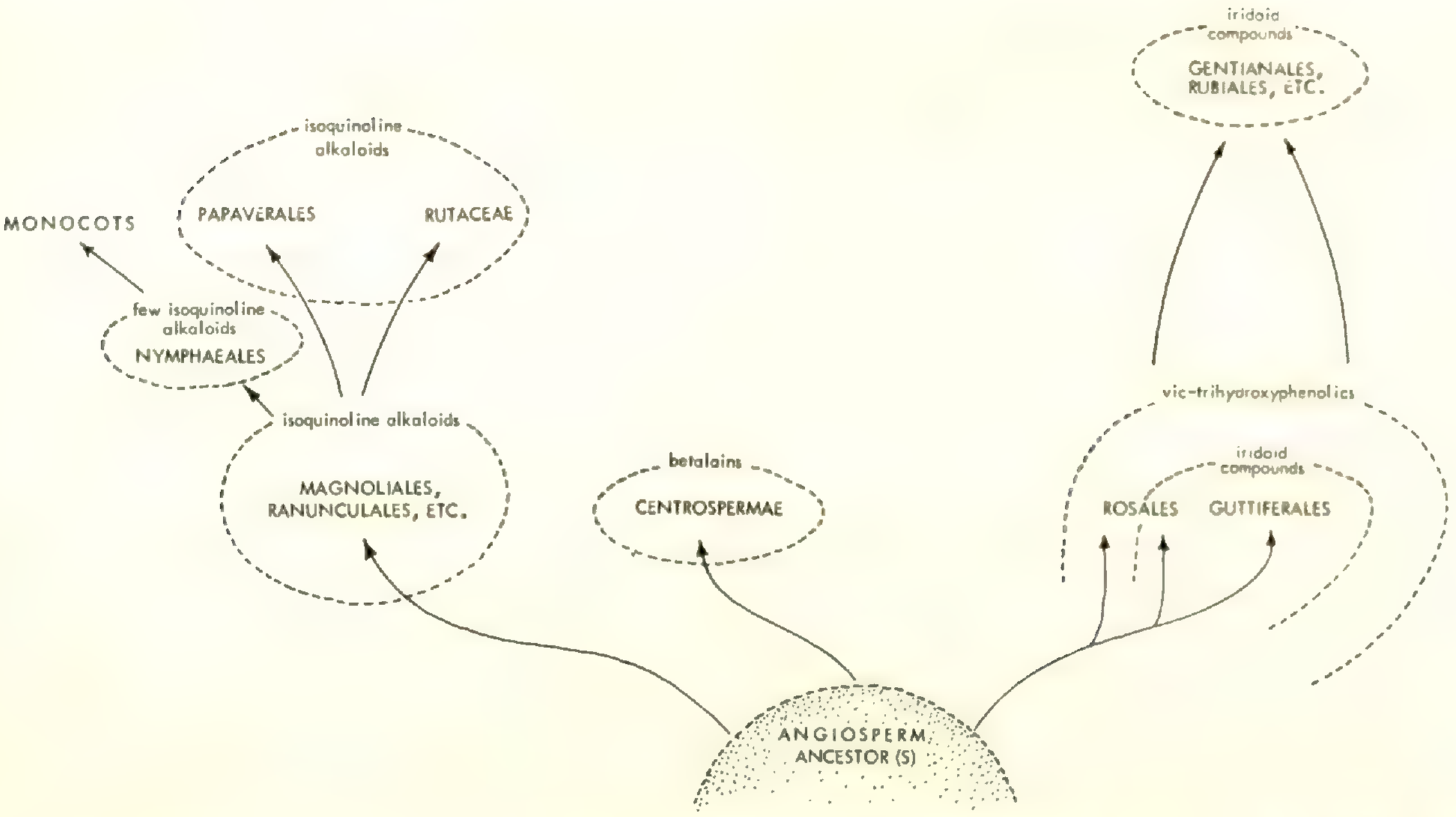

FIGURE 11. A scheme for the origin of major lines of dicotyledons based in part upon the distribution of selected natural products (adapted from Kubitzki, 1969; see also Figs. 8–10).

Nymphaeales (Bate-Smith, 1968) does not support the similar views of Cronquist and Takhtajan that a dicotyledon group such as the Nymphaeales could have given rise to the monocots. Hegnauer has privately expressed his view with regard to this matter as follows: "If we look for chemical resemblances between monocots and dicots, we find most of them if we look at Liliiflorae, Magnoliales and Ranunculales. . . . I expect that a connection between the two classes of angiosperms will ultimately be found here."

Kubitzki (1969, 1972), who superimposed upon Cronquist's interpretation of the evolutionary relationships of the dicotyledons the distribution of ellagic acid (Fig. 8), isoquinoline alkaloids (Fig. 9), and iridoid compounds (Fig. 10), suggested that the chemical data indicated that the Rosales and Theales both have primitive characters and evolved parallel to the ranalian (s.l.) and centrospermoid lines (Fig. 11).

The presence of ellagic acid and iridoid[9] compounds in many families related to the Rosales and Guttiferales and their absence from the isoquinoline alkaloid-containing ranalian group indicates that the former were almost certainly not derived from the ranalian complex as suggested by Takhtajan and Cronquist but instead represent independent lines. Further evidence that the ability to synthe-

[9] The name iridoid is derived from *Irodomyrmex*, a genus of ants in which these terpenoid-derived plant products also occur.

←

Mues & Zinsmeister, 1973).—9. Distribution of isoquinoline alkaloids. Aporphine is a typical isoquinoline alkaloid. Solid line = quaternary bases magnoflorin, berberin, and menisperin; broken line = protoaporphine and aporphine.—10. Distribution of iridoid compounds (see Wieffering, 1966). Aucubin is a typical and well known iridoid.

TABLE 4. Genera of Compositae reported to contain sesquiterpene lactone; arranged by tribes.

Vernonieae	*Elephantopus, Vernonia*
Eupatorieae	*Eupatorium, Mikania, Stevia*
Inuleae	*Carpesium, Geigeria, Inula, Telekia*
Heliantheae	*Ambrosia, Balduina, Cosmos, Encelia, Helianthus, Hymenoclea, Iva, Parthenium, Polymnia, Xanthium, Zaluzania, Zexmenia*
Helenieae	*Bahia, Baileya, Eriophyllum, Gaillardia, Helenium, Hymenoxys, Psilostrophe*
Anthemideae	*Achillea, Anthemis, Artemisia, Chrysanthemum, Matricaria*
Senecioneae	*Petasites*
Calenduleae	*Cnicus, Jurinea*
Cynareae	*Amberboa, Arctium, Centaurea, Cynara, Onopordon, Saussurea*
Cichoreae	*Cichorium, Hyenanche, Lactuca, Sonchus, Urospermum*

size ellagic acid developed early in the course of evolution is the interesting discovery of this substance in liverworts (Mues & Zinsmeister, 1973).

CYANOGENIC GLUCOSIDES

Cyanogenic glucosides are a group of natural products which are derived from amino acids; they have the ability to release hydrogen cyanide (cyanogenesis) upon treatment with acids or appropriate enzymes.

The pattern of distribution of cyanogenesis, which has been reported from over 800 species in 70 different plant families (see Eyjolfsson, 1970), indicates frequent independent origin of cyanogenic glucosides. Nevertheless, in a few instances, the data appear to bear upon the interpretations of Cronquist and Takhtajan for certain groups.

For example, Cronquist places *Sambucus* in the family Caprifoliaceae while Takhtajan does so questioningly. The available chemical evidence favors Takhtajan and others who have considered the group as a distinct family, Sambucaceae. *Sambucus* contains the cyanogenic glucoside sambunigrin, which represents the only report of this class of natural products in the Caprifoliaceae (see Glennie, 1969). Furthermore, *Sambucus* does not contain dicaffeoyl-quinic esters, which are widespread in other genera of the Caprifoliaceae (Glennie, 1969).

Cronquist treated two families, Passifloraceae and Flacourtiaceae (both of which contain similar cyanogenic glucosides), as being closely related and placed them together in the order Violales; in contrast, Takhtajan, while recognizing their similarities ("it is very difficult to draw a clear taxonomic boundary between

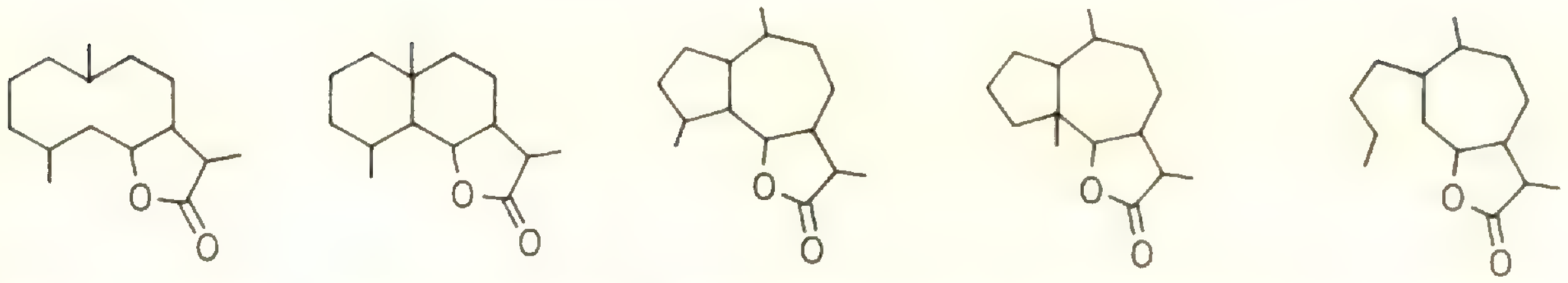

FIGURE 12. Five biogenetically-related skeletal types of sesquiterpene lactones which characterize most tribes of the family Compositae.

the Passifloraceae and the Flacourtiaceae"), nevertheless placed them in different orders, albeit closely related.

SESQUITERPENE LACTONES

Of the several hundred reports of the occurrence of sesquiterpene lactones in higher plants, more than 75% are from the Heliantheae, Helenieae, and Anthemideae, three tribes of the Compositae, Table 4 (see Yoshioka et al., 1973). In addition, virtually all other tribes in the Compositae contain one or more of the five or so biogenetically related types of sesquiterpene lactones which characterize the Heliantheae-Helenieae-Anthemideae complex (Fig. 12), indicating that the Compositae is a highly integrated natural assemblage.

Of more interest here are the accounts of sesquiterpene lactones in taxa outside the Compositae, especially in light of the recent cytochrome *c* results which indicate that this family is much older than previously thought (see Turner in GENERAL SUMMARY AND CONCLUSIONS). Both Cronquist and Takhtajan suggest similar origins for the Compositae; namely, from the Rubiales-Dipsacales[10] and Calycerales-Campanulales, respectively.

Of the 16 genera of angiosperms outside the Compositae which are known to contain sesquiterpene lactones, only those substances from the primitive families Magnoliaceae and Lauraceae appear to be biogenetically similar to those which are found in the Compositae. Indeed, *Michelia* (Magnoliaceae) and two species of the Compositae, *Ambrosia dumosa* and *A. confertiflora*, produce the very same substance (parthenolide); these data support the view that the Compositae are an older group than previously supposed[11], possessing relationships that presumably extend back to the magnolioid lines.

Two families which have similar sesquiterpene lactones, the Coriariaceae and Menispermaceae, are aligned together in the Ranunculales by Cronquist, while Takhtajan places the Coriariaceae in the Rutales with the comment that "family relationships are not clear."

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[10] It is interesting to note that one of Cronquist's comments in connection with choosing the Rubiales-Dipsacales ancestral route for the Compositae rather than the Campanulales will, I believe, prove not to be true, namely, the statement that "phenolic compounds are widespread in the Compositae and are also present in many Rubiales and Dipsacales, whereas, they are unknown in the Campanulales."

[11] In this connection, it might be noted here that C-glycosylflavones, considered by some (see Harborne, 1972) to be primitive substances because of their occurrence in mosses, liverworts, and even a green alga, are being found in an increasing number of Compositae genera.

ALKALOIDS

Perhaps 20% or more of the vascular plants contain one or more alkaloids (see Willaman & Li, 1970) and in many instances, these nitrogen-containing toxic substances have phylogenetic significance at higher taxonomic levels. Thus their distribution patterns often bear upon the interpretations of Cronquist and Takhtajan for certain families (see Hegnauer, 1963, 1967).

In applying the distribution of alkaloids for phylogeny it is essential to recognize that they are derived from amino acids by a variety of biosynthetic pathways and the mere presence or absence of "alkaloids" can not be used as a rigorous phyletic marker in the way, for example, one uses the distribution of the biogenetically homogenous leucoanthocyanidins.

The overall distribution of the isoquinoline alkaloids suggests that the major evolutionary lines of dicotyledons as proposed by both Cronquist and Takhtajan are incorrect (see Fig. 9 and the relevant discussion in the section PHENOLICS). The presence of aristolochic acid (which appears to be a structurally advanced modification of the isoquinoline alkaloids) in the Aristolochiaceae suggests that this group is an advanced member of the Magnoliidae in accord with the treatments of both Takhtajan and Cronquist.

Although Cronquist and Takhtajan differ in a number of ways in their interpretations of the Asteridae, one particularly interesting difference concerns their treatments of the Rubiaceae. The Rubiaceae is allied with the Loganiaceae and Apocynaceae in the Gentianales by Takhtajan; his view is strongly supported by the similar complex tryptophan-terpene-derived indole alkaloids which are produced in large numbers by many members of all three families. In contrast, Cronquist, while recognizing the relationship of the Loganiaceae to the Rubiaceae ("In my opinion the Loganiaceae are near-ancestral to the Rubiaceae. . . ."), placed the Rubiaceae in a distinct order.

CONCLUDING STATEMENT

During the course of the preparation of this manscript the writer's view with regard to the potential of natural products as an aid for understanding the phylogeny of major evolutionary lines of angiosperms was appreciably altered. I had generally believed that the data were insufficient to do more than hint at a meaningful arrangement of the higher categories; now, however, I am convinced that a more thorough evaluation of the presently available information for the distribution of biogenetically related natural products in conjunction with a re-interpretation of all other data will give considerable new insight into family and order relationships. Such an undertaking is presently being planned.

MACROMOLECULES—SYSTEMATIC SEROLOGY

Biologists have known for approximately 75 years that organisms may share antigenic material (substances capable of inducing the formation of antibodies and able to react with the antibodies), and when they share the same antigenic material in different proportions it is assumed that the organisms are related.

Most of the phytoserological research has encompassed what is designated

comparative serology. The basic methods for serosystematic or serotaxonomic research involve the immunization of experimental animals to induce antibodies (serum globulins) followed by the analysis of the reaction of the antibodies so produced with properly prepared antigenic material. This type of research can be conducted employing quantitative precipitation (precipitin) techniques in solutions (Boyden procedure, Moritz procedure, quantitative ring precipitation reaction), or by various qualitative precipitation techniques in gels (Oudin method, Ouchterlony method, double diffusion, and immunoelectrophoresis). Thus immunological techniques provide one kind of measurement of the protein similarities among taxa.

The precipitin reaction has a history dating from the time of Kraus (1897). The precipitin reaction has been used in taxonomic research since Nuttall (1901) published his new biological test for blood in relation to classification. Some precipitin reactions are used as an index for determining degree of serological correspondence, which is a summation of the immunological reactions throughout the antigen reaction range. The detected and measured similarities are based on the structure (amino acid sequences and molecular configurations) of the determinant groups, which are the portion of the antibody molecule that reacts or combines with a portion of the antigenic molecule. Such portions of the single antigenic molecule as are "reprinted" by the specific portion of the antibody molecule are designated "determinant groups," "determinant sites," or "determinants" (Fairbrothers, 1968, 1969, 1970). Fairbrothers (1969, 1972) reported that approximately 520 plant taxa (from cultivars through orders) have been included in approximately 150 systematic serological publications in the last 25 years. Research has demonstrated that extracts of seeds, pollen, leaves, tubers, and spores of vascular plants can be used, if the required extraction procedures are followed (Fairbrothers, 1969, 1971). Most of the vascular plant immunological studies have included extracts containing multiple antigen-antibody systems. This is why absorption techniques (removing common immunoprecipitating systems and leaving only those systems specific for each taxon compared) help reveal a measure of the relative similarity.

The terms reference antigenic material, cross-reacting antigenic material, reference reaction, and cross-reaction are frequently used in systematic serological publications (Fairbrothers, 1968). Reference antigenic material is the material used to immunize the antibody producers. Reference reaction is the reaction between an antiserum and the antigenic material used to stimulate its formation, and is the standard reference in comparative research. Cross-reacting antigenic material is material other than the reference antigenic material which will react serologically with the antibodies. Cross-reaction is the reaction between an antiserum and any antigenic material other than that used in its formation.

The following three generalizations have resulted from evaluating an array of systematic serological research: (1) The amounts of serological correspondence among proteins decrease with decreasing systematic relationships. (2) The amounts of serological correspondence are in accord with known genetic relationships. (3) Serological correspondence obtained by different antigenic material gives consistent relative systematic placements (Boyden, 1966).

While evaluating the contribution of serological data related to Cronquist's and Takhtajan's systems of classification, it became evident that I should refer to selected developing phases of each of the two systems. Thus by comparing Cronquist's (1957, 1965, 1968) and Takhtajan's (1959, 1969) publications it was possible for me to more accurately assess the role of serological data as the authors modified the two systems of classification. I did not compare the selected publications of each author to prove they changed their interpretations, but rather to determine how serological information was incorporated in their revisions.

MAGNOLIALES AND ILLICIALES

Johnson's (1953, 1954) and Johnson & Fairbrothers's (1964, 1965) information indicated that *Liriodendron* produced serological reactions which isolate the genus as a monotypic tribe or subfamily in the Magnoliaceae, a view shared by both Cronquist and Takhtajan. Serological data (Johnson, 1953, 1954; Johnson & Fairbrothers, 1964) comparing species of *Illicium* and *Schisandra* support those classifications which transfer the two genera from the Magnoliaceae to two separate families (Cronquist, 1968), or even to a separate order Illiciales (Illiciaceae and Schisandraceae) as proposed by Takhtajan (1969). Taxa of the Illiciaceae and Schisandraceae had greater serological similarity with each other than either family had with tested genera of the Magnoliaceae.

RANUNCULALES

Hammond (1955), Jensen et al. (1964), and Jensen (1968a) all determined that the genus *Paeonia* had very little or no serological affinity with taxa of the Ranunculaceae. Hammond (1955) also indicated a serological correspondence between *Hydrastis* and taxa of the Ranunculaceae, although several botanists would exclude this genus from the family. Jensen (1966, 1967, 1968a) indicated *Hydrastis* had little serological correspondence with the Berberidaceae (including Podophyllaceae) and greater correspondence with the Ranunculaceae. Thus the serological data supports Takhtajan's (1969) and Cronquist's (1968) family Paeoniaceae and its inclusion in a separate order from the Ranunculaceae, but the data would not support Takhtajan's inclusion of *Hydrastis* in a monotypic family Hydrastidaceae, or his statement that the genus is intermediate between the Ranunculaceae and the Podophyllaceae (Berberidaceae). The genera *Nigella* and *Erianthis* both are serologically isolated in the family Ranunculaceae (Jensen, 1968a, 1968b).

Jensen (1974) conducted a serological comparison of seed proteins of 12 genera of the Berberidaceae. He reported a high degree of serological similarity between *Mahonia* and *Berberis* (indicating one genus), and also between *Podophyllum* and *Diphyleia*. His data did not support those classifications which separate the genus *Nandina* from the Berberidaceae. *Nandina*, *Berberis*, *Mahonia*, *Podophyllum*, and *Diphyleia* formed one grouping (subfamily?). *Achlys*, *Bongardia*, *Caulophyllum*, *Epimedium*, *Jeffersonia*, *Leontice*, and *Vancouveria* formed another grouping (subfamily?). However, the serological similarities among the taxa forming the second grouping were not as close as were those genera forming the first grouping (Jensen, 1974). Cronquist (1968) placed all the genera in the

one family Berberidaceae, while Takhtajan (1969) placed the genera in the three families: Podophyllaceae, Nandinaceae, and Berberidaceae. However, Takhtajan in a printed discussion following Jensen's (1974) article stated that a recently published paper written by Melikian and Takhtajan indicated that all the genera should be placed in three subfamilies within the Berberidaceae.

CAPPARALES AND PAPAVERALES

The serological investigation of the Rhoeadales (Jensen et al., 1964) demonstrated that this order was composed of two distinct groups. One group, the Papaverales (Papaveraceae and Fumariaceae), revealed serological correspondence with the Ranunculales. The other group, the Capparales (Capparaceae and Cruciferae), stands apart serologically from the Papaverales and the Ranunculales. Cronquist (1957) stated that the four families formed a natural order; however, in 1965 he indicated it might be best to divide the order. In 1968 he listed two orders, the Papaverales and Capparales, and expressed the same relationships revealed by the serological data. Takhtajan (1969) also indicated the same orders and relationships in his classification as detected by the serological data.

CARYOPHYLLALES

Jensen (1965) and Moritz (1966) reported serological data which clarified the taxonomic position of the Didiereaceae, an endemic family of the arid regions of southwest Malagasy Republic (Madagascar). The systematic position of these cactus-like, thorny shrubs and trees has been controversial for approximately 80 years. Cronquist (1957) placed the Didiereaceae in the Euphorbiales. However, in 1965 he cited the betacyanin data (Rauh & Reznik, 1961; Mabry, 1964) and indicated that the family might ultimately be included in the Caryophyllales. Takhtajan (1959) gave some indication of taxonomic affinity with the Nyctaginaceae.

Jensen (1965), using the antisera from the genus *Alluaudia* of the Didiereaceae to test 23 antigenic systems derived from taxa usually placed in the Caryophyllales (Centrospermae) and 11 antigenic systems of non-Caryophyllales, clearly demonstrated strong serological correspondence between the Didiereaceae and tested members of the Caryophyllales. Statements by Cronquist (1968) and Takhtajan (1969) clearly indicated that the serological data were important in their placement of the Didiereaceae in the order Caryophyllales, as well as in establishing the position of the family in regard to other families included in that order.

CORNALES

The order Cornales (Cornaceae, Davidiaceae, Garryaceae, and Nyssaceae) has been investigated serologically for 10 years (Fairbrothers & Johnson, 1964; Fairbrothers, 1966a, 1966b, 1966c, 1968). The data have shown that the genus *Cornus* is divisible into serological groupings. Data have also illustrated a serological correspondence among species of *Cornus, Davidia, Garrya*, and *Nyssa*. Data obtained from quantitative and qualitative immunochemical techniques indicated very little or no serological correspondence of *Corokia* (Cornaceae) with any tested taxa belonging to the Cornales.

The placement of *Nyssa* in the Nyssaceae and *Davidia* in a subfamily of the Nyssaceae or as a separate family Davidiaceae, *Cornus* in the Cornaceae, *Garrya* in the Garryaceae, and *Corokia* removed from the Cornales, best expressed the serological data. Serologically *Davidia* is most similar to *Nyssa*, *Nyssa* is most similar to *Cornus*, and the Garryaceae is the most isolated of the four families.

The serological data support Cronquist (1968) who did not include the Araliaceae and Umbelliferae in the Cornales as did Takhtajan (1969). Takhtajan excluded the genus *Corokia* from the Cornales and placed it in the Escalloniaceae (Saxifragales). Cronquist discussed the status of *Corokia* as a possible non-missing link between the Cornaceae and Escalloniaceae, Grossulariaceae, or Saxifragaceae sensu lato. Both treatments reflect the serological data which indicated the distinctiveness of *Corokia* from members of the Cornales.

Rodriguez (1971) compared the data from diverse disciplines (including serological) and discussed the indicated relationships for members of the Cornales.

UMBELLALES

The analyses of data obtained from extracted seed proteins of 13 genera of the Umbelliferae employing the Boyden procedure and Ouchterlony technique (double diffusion) revealed three distinct serological groupings. These groupings essentially correspond to the three subfamilies. The data also indicated that one grouping (Apioideae) was more similar to the Saniculoideae than to the Hydrocotyloideae (Pickering & Fairbrothers, 1970). Seventeen taxa of the subfamily Apioideae were investigated serologically and five major groupings were detected which correspond to five tribes. Other serological groupings revealed a relationship suggested by some of the designated taxonomic subtribes of the Apioideae (Pickering & Fairbrothers, 1971).

Varying degrees of protein similarity have been obtained among members of the Araliaceae, Cornaceae, Garryaceae, Nyssaceae, and Umbelliferae. These preliminary data indicate a possible common ancestral complex for these five families (Hillebrand & Fairbrothers, 1970a, and unpublished data).

LAMIALES, POLEMONIALES, AND SCROPHULARIALES

The Scrophulariaceae is generally considered by taxonomists to be the family most nearly related to the Solanaceae (Hawkes & Tucker, 1968). The genus *Schizanthus* has been placed in both the Scrophulariaceae and Solanaceae. Hawkes & Tucker (1968) in their extensive serological assessment of relationship within the family Solanaceae have also made preliminary comparisons with taxa of the Scrophulariaceae, Boraginaceae, Convolvulaceae, and Leguminosae. For the inter-family comparison they used antisera prepared to *Schizanthus*, a genus serologically isolated in the Solanaceae, and *Salpiglossis*, a genus strongly reacting serologically with other genera of the Solanaceae. The Boraginaceae and Convolvulaceae taxa produced extremely faint or no serological reactions with taxa of the Solanaceae. All the Scrophulariaceae taxa produced faint cross-reactions with the Solanaceae, which Hawkes & Tucker (1968) interpreted as an indication of some relationship between the two families.

Cronquist (1968) placed the Solanaceae in the same order as the Convolvulaceae (Polemoniales), Boraginaceae in another order (Lamiales), and the Scrophulariaceae in still another order (Scrophulariales). Takhtajan (1969) placed the Solanaceae and Scrophulariaceae in the order Scrophulariales, and the Convolvulaceae and Boraginaceae in the order Polemoniales. Takhtajan's arrangement better reflects the serological data reported by Hawkes & Tucker (1968).

DIPSACALES AND RUBIALES

A serological investigation of intrageneric relationships in *Viburnum* revealed that the genus was a taxon distinct from all others tested. However, serological groupings would support the division of the genus into taxonomic subgroupings (subgenera, sections). Representatives of the most primitive taxonomic grouping of the genus displayed the least serological reactivity with the most advanced taxonomic grouping (Hillebrand & Fairbrothers, 1969).

A three-dimensional model illustrating serological correspondence among five tribes of the Caprifoliaceae and the families Cornaceae and Nyssaceae indicated the following: (1) Tribes Lonicereae and Diervilleae were very similar. (2) Linnaeae was close to the Lonicereae and Diervilleae. (3) The families Cornaceae and Nyssaceae and the tribe Sambuceae were approximately equally similar to the above three tribes. (4) Viburneae was serologically removed from the other four tribes and two families, but most similar to Sambuceae. (5) *Cornus*, *Nyssa*, and *Sambucus* were more similar to each other than to any other members tested. (6) The families Cornaceae and Nyssaceae were as similar or more similar serologically to the three tribes of the Caprifoliaceae than the three tribes were to the Viburneae and Sambuceae of the Caprifoliaceae (Hillebrand & Fairbrothers, 1970a).

The serological correspondence of the Cornaceae and Nyssaceae with most representatives of the Caprifoliaceae, especially *Sambucus*, contrasts with the very low or negative correspondence of genera of the Caprifoliaceae (including *Sambucus* and *Viburnum*) with the Rubiaceae; this indicates a closer protein similarity between the Caprifoliaceae, Nyssaceae, and Cornaceae than between the Rubiaceae and Caprifoliaceae (Hillebrand & Fairbrothers, 1970b). Cronquist (1968) placed the Rubiaceae in the monotypic order Rubiales, and the Caprifoliaceae (including *Sambucus* and *Viburnum*) in the order Dipsacales. He concluded that, depending on how the evidence is weighed, the Rubiaceae could be included in the Dipsacales, Gentianales, or placed in a monotypic order. He interpreted the serological evidence as indicating that the nearest common ancestry of the Caprifoliaceae and Cornaceae would be in the Rosales. Hillebrand & Fairbrothers (1965), based on serological data, alluded to such a possibility. Takhtajan (1969) included the Caprifoliaceae in the Dipsacales and placed *Sambucus* in the Caprifoliaceae with a question mark. He also indicated that the Dipsacales was related to the Cornales, and that the Caprifoliaceae exhibits definite links with the Cornales. He placed the Rubiaceae in the order Gentianales and indicated that this order has a common origin with the Dipsacales.

The serological data are best reflected by Takhtajan's classification. However,

both systems of classification have not adequately dealt with the chemical information available for either *Sambucus* or *Viburnum*. Both systems reflect the serological data which indicated that the Caprifoliaceae and Rubiaceae are not as taxonomically similar as has been traditionally indicated.

PRE-MONOCOTYLEDONOUS DICOTS

Cronquist (1968) and Takhtajan (1969) both indicated that the monocotyledons originated very early and that their ancestors were primitive dicotyledons most like the Nymphaeales. Takhtajan indicated that the Nymphaeales have been classified both as dicotyledons and monocotyledons. Cronquist (1968) placed the Nelumbonaceae and Nymphaeaceae in one order (Nymphaeales) and Takhtajan (1969) placed the two families in separate orders (Nelumbonales and Nymphaeales). Simon's (1970, 1971) serological data indicated that *Nuphar* and *Nymphaea* were close and *Nelumbo* was isolated from these two; thus Takhtajan's treatment best expressed the serological information. Serological affinities were also detected between Nymphaeales, Magnoliales, Laurales, and Ranunculales. The Nymphaeales antisera also produced partial identity reactions with taxa of five monocotyledon families belonging to three orders. These data support the suggested pre-monocotyledonous dicot affinity with nymphaeous-like plants.

TYPHALES

Diverse placement of the order Typhales (Sparganiaceae and Typhaceae) within the monocotyledons indicates disagreement about the origin and evolutionary history of the order. Hutchinson (1959) indicated the order originated from the primitive Liliales. Cronquist (1968) placed the Typhales in the subclass Commelinidae and postulated a generalized commelinalean ancestry. Takhtajan (1969) viewed the Typhales as having developed in a long evolutionary line from plants which preceded the Liliales, and placed it in the subclass Arecidae. He also indicated evolutionary affinities between the Typhales and Pandanales. Stone (1972) reported that his investigations of the Pandanaceae indicated little affinity with the Typhaceae, and suggested that postulated relationships between the two families resulted from superficial resemblances. Other classifiers have indicated relationships with the Palmae, Arales, Alismatales, Commelinales, etc.

A serological investigation of the Typhales (Lee & Fairbrothers, 1972) indicated the following: (1) significant serological correspondence between *Typha* and *Sparganium*, thus making the placement of the two families in one order appropriate, (2) low serological correspondence between the order and several Liliales, indicating possible distant evolutionary relationship, (3) negative or no significant serological affinity with Araceae, Commelinaceae, Cyperaceae, Gramineae, Juncaceae, Palmae, and Pandanaceae.

Lee and Fairbrothers (1972) suggested as a working hypothesis that the Typhales originated in the primitive or ancestral Liliales. It would then be placed in Cronquist's and Takhtajan's subclass Liliidae. However, serological data reflected (as do all other data) an extremely isolated position for the Typhales within the monocotyledons.

CONCLUSIONS

Researchers employing both quantitative and qualitative immunological techniques have obtained valuable additional and/or complementary data for taxonomic investigations. Phytoserological research has also provided provocative and valuable chemical characteristics for use in the classification of higher plants; and in some research immunological data have transcended in significance data available from other characters. The examples presented clearly indicate that serology has contributed chemical data which have been used, in conjunction with other data, to produce the Cronquist and Takhtajan systems of classification and which could be used to refine these systems. The increased use of such data in classification only awaits the increased production of comparative phytoserological research.

Macromolecules—Amino Acid Sequences

The realization that the amino acid sequences of homologous proteins in different taxa contain phylogenetically useful information derives from advances in molecular biology during the past several decades. The appreciation that a particular nucleotide sequence in the genome (a structural gene) programs for a unique amino acid sequence in a protein led Zukerkandl & Pauling (1965) to note with characteristic insight that knowledge of the amino acid sequences of genetically homologous proteins from different species permits reconstruction of the evolutionary history of, at the least, single genes. Zoologists have rather widely used the comparison of amino acid sequences to illuminate phylogenetic relationships among animals, but only very recently have the data become available to apply this approach to the study of phylogeny within the plant kingdom. By way of introduction to this topic, selected aspects of the use of amino acid sequences in phylogenetic studies are discussed below.

Rationale.—Two phylogenetically related taxa shared a common ancestor at some point in time, earlier or later depending on their degree of relatedness. Homologous structural genes common to these taxa have descended by fixation of point mutations from a nucleotide sequence in their common ancestor. The degree of similarity of the nucleotide sequences in the genomes of the two organisms is a measure of the extent of their divergence from the common ancestor and of their phylogenetic relatedness. At present it is technically impossible to rigorously and directly assay the similarity of two entire genomes or even single homologous genes embedded in those genomes (DNA-DNA hybridization techniques and sequencing of small nucleic acids notwithstanding). Since a nucleotide sequence programs for a unique amino acid sequence, it is possible to assay the similarities of two homologous genes indirectly by comparison of their gene product, the protein. Thus the comparison of amino acid sequences among homologous proteins allows evaluation of degree of relatedness among several taxa.

Assumptions.—It is assumed that the structural genes programming the particular protein whose sequences among several taxa are being compared are evolutionally homologous. Two other sources of sequence similarity exist: (1) random chance and (2) evolutionary convergence in which constraints imposed by the biochemical function of the protein allows only certain amino acid

sequences (analogy). The former of these two sources can be detected with statistical tests (Fitch, 1970). The latter possibility cannot be rigorously excluded, but semi-rigorous statistical tests indicate that the cytochromes *c* of animals and fungi are evolutionally homologous (Fitch & Markowitz, 1970) and an analysis yielding similar results for plant cytochromes *c* has been performed (Ramshaw & Brown, unpublished).

Additional assumptions are tacit in the method used in the construction of the phylogenetic tree from sequence data. For a discussion of these the reader is referred to Boulter et al. (1972).

Weaknesses.—A phylogeny based on the comparison of amino acid sequences of a protein is the phylogeny of a structural gene, not necessarily of species. To the extent to which changes within that gene reflect the evolution of the organism possessing that gene, this approach is valid. If the rate of change in a gene is linear in time and relatively slow, sudden bursts of morphological change accompanying adaptive radiations may not be reflected in gene products. In such cases a phylogeny constructed on a single gene will yield a correct, but incomplete topology. Alternatively phrased, variation in morphology need not necessarily be reflected in all gene products. This problem was considered by Simpson (1964). He noted that the closer one gets to DNA in the process of transcription of genetic information, the farther one gets from the "cutting edge" of natural selection, namely, the phenotype. Due to the technical difficulties inherent in protein sequencing, phylogenetic trees derived from protein comparisons will be based on a relatively few structural genes for some time to come.

A practical problem arises in that each protein (i.e., gene) appears to have a characteristic evolutionary rate (about which more will be said below) determined in part by the biological role of the molecule. Therefore, the rate of change of one protein (e.g., cytochrome *c*) might make that protein very useful for familial comparisons and useless at the generic level. The converse is observed in other, more variable proteins. So the particular protein must be carefully selected for a comparative study at a given taxonomic level.

Strengths.—The construction of a phylogenetic tree based on amino acid sequences and using the ancestral sequence method permits the reconstruction of a precise, quantitative, and objective topology of relationships. At the taxonomic level for which that protein is validly used, a sequence comparison will demonstrate the order in which each group represented diverged from the common ancestor with its phylogenetic neighbors. As discussed further below, a time scale for such divergences may be appended to such a tree.

Comparative sequence data are highly amenable to increasingly sophisticated statistical analysis. Statistical techniques are being developed to detect and eliminate such potential sources of errors as back mutations, double mutations, redundancy in the genetic code, and convergent biochemical evolution (Fitch & Margoliash, 1969).

Comparison of amino acid sequences yields some insights into the actual molecular mechanism of the evolutionary process. For example, the currently controversial topic of the random fixation of selectively neutral mutations is largely a spin-off of comparative protein sequence data.

Why Use Comparative Sequence Data for Plants?—*A priori*, there is no compelling reason to place much confidence in a phylogenetic history of the higher plants based on a single structural gene within the huge genome of modern angiosperm taxa. Why then should botanists believe a phylogenetic tree based on amino acid sequences of a single (albeit homologous) protein among several plant families? The sole answer is simply that in the animal kingdom, for which a clear-cut fossil record exists for the general pattern of vertebrate evolution, a phylogenetic scheme based on the cytochrome *c* gene mimics almost perfectly such a tree constructed on the basis of the extensive fossil record. In the absence of a well preserved fossil record, angiosperm phylogenists must assume that phylogenies based on comparisons of amino acid sequences from homologous proteins in plants are fairly accurate. This acceptance is based on the zoologist's experience and we operate somewhat under the dictum attributed to Thomas Edison, who, when pressed as to the basic nature of electricity is reported to have replied: "Electricity is, use it."

METHODS

The techniques for protein purification and amino acid sequence determination are legion, lengthy, laborious and well reviewed elsewhere (Blackburn, 1970; Needleman, 1970). The sequencing techniques, per se, do not bear upon the biological arguments and no purpose would be served treating them here.

DISCUSSION

Currently Available Data.—A picture is emerging of evolution at the molecular level which suggests that each protein evolves (i.e., accepts point mutations) at a constant and characteristic rate. For cytochrome *c* the number of accepted point mutations per 100 amino acid residues each 100 million years is 3; for the much more conservative protein histone IV, 0.06; for the highly variable fibrinopeptides, 90 (Dayhoff, 1972). This characteristic rate of evolution for a particular protein defines the taxonomic category at which the comparison of amino acid sequences will be phylogenetically fruitful. The most "conservative" proteins (e.g., histones) are useless for phylogenetic studies because they are virtually invariant across entire kingdoms. "Moderately conservative" proteins such as cytochrome *c* and hemoglobin are useful at higher (ordinal and familial) levels. Highly variable proteins will be more useful at the lower levels of specific and generic comparisons.

Cytochrome *c* evolves at a rate such that comparisons of its sequences are useful at the familial level. The two congeners, *Brassica oleracea* and *B. napus*, have been shown to have identical cytochrome *c* amino acid sequences (Richardson et al., 1971; Thompson et al., 1971) and members of the same family (*Gossypium* and *Abutilon*, *Helianthus* and *Niger*) have very similar sequences (Boulter, 1973). Because of its useful rate of evolution and other reasons (size, ubiquity of occurrence, relative ease of purification, optical properties) mitochondrial cytochrome *c* is one of the most widely sequenced of all proteins.

Only two proteins, cytochrome *c* and ferredoxin, have been purified and sequenced from a sufficient number of different angiosperms to permit com-

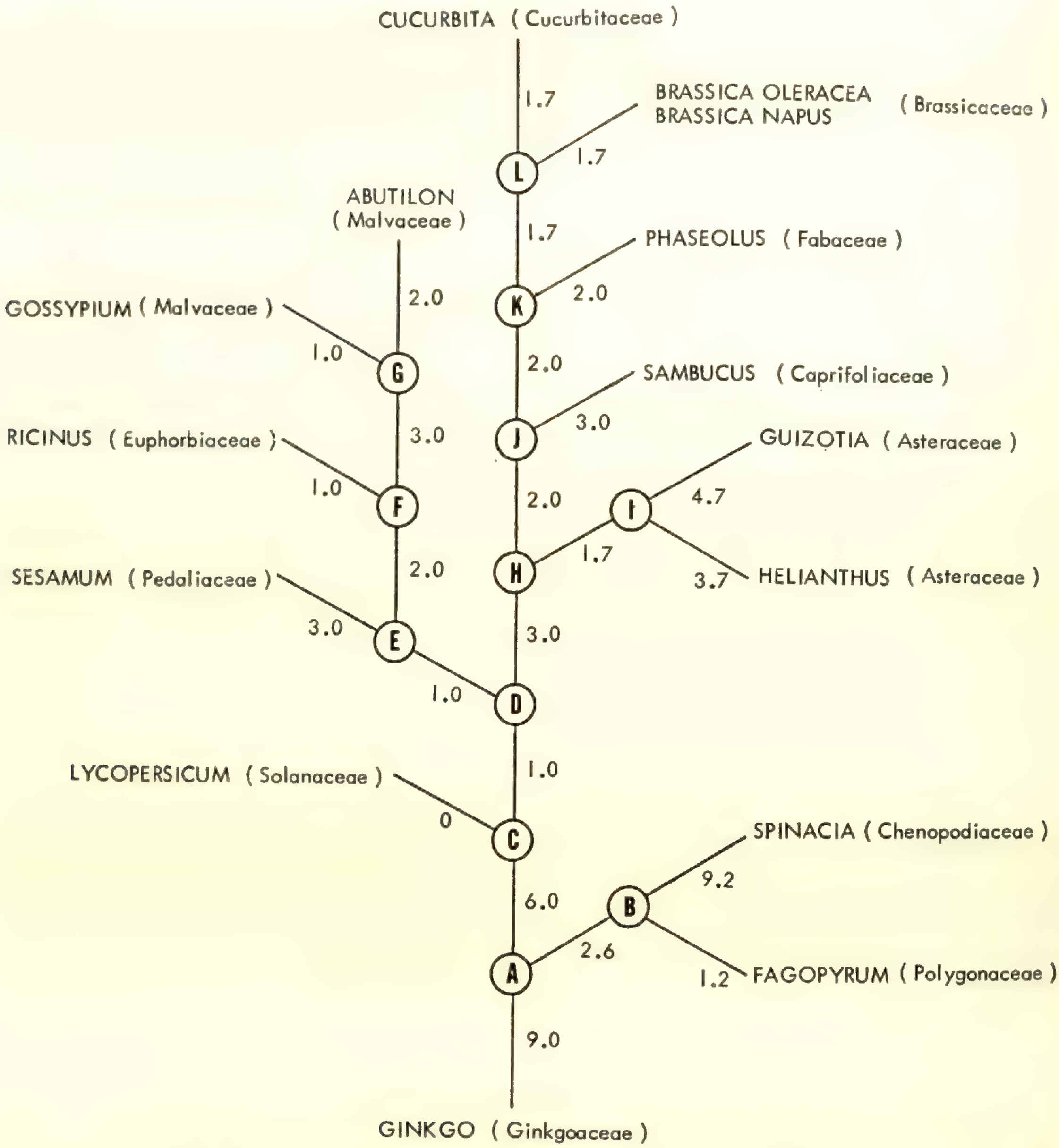

FIGURE 13. A phylogenetic tree relating fifteen plant species, constructed using the "ancestral sequence" method. Numbers refer to the "average" amino-acid difference between the nodes A–L and lineages concerned. (After Boulter et al., 1972).

parisons of sequences and construction of preliminary phylogenies. The amino acid sequence of the respiratory electron transport protein, mitochondrial cytochrome *c*, has been reported from 19 angiosperm species (Boulter, 1973; Brown et al., 1973; Brown & Boulter, 1973). As yet unpublished sequences are known from several algae (B. T. Meatyard, unpublished) and several additional monocots (D. Richardson, unpublished). These data have recently been used to construct a phylogenetic tree of the higher plants based on the cytochrome *c* gene (Boulter et al., 1972) and this tree is shown in Fig. 13. Although based on a single gene in the 15 species, this tree is remarkably similar to more traditionally derived trees based primarily on morphological considerations.

In comparing the relationships derived from comparison of cytochrome *c* sequences with existing classification schemes it is noted that the clustering of related families is virtually identical. If the superorder Malvanae of the Takhtajan scheme were transferred from the subclass Dilleniidae to the subclass Asteridae, virtual congruence with the cytochrome *c* tree would be achieved.

At present too few sequences from too few families are known to resolve any but the most general outlines of angiosperm phylogeny. As more sequences are accumulated, the confidence in, resolving power of, and contribution of phylogenetic trees based on amino acid sequences should greatly increase.

To the extent to which molecular evolution in proteins is constant and linear in time, trees based on amino acid sequences permit the attachment of a time scale for the divergence of major groups from their ancestral stocks. Such a time scale has recently been examined (Ramshaw et al., 1972) based upon the known cytochrome *c* sequences.

The only other plant protein of possible phyletic significance in the near future is the photosynthetic electron carrier, ferredoxin. The amino acid sequence of ferredoxin has been determined from four angiosperms (Dayhoff, 1972). Comparison of these known sequences allows no phyletic deductions among these taxa at present. The number of amino acid substitutions between two members of the same family (*Medicago sativa* and *Leucaena glauca* with 24 residues different) is greater than the differences between a dicot and a monocot (e.g., *L. glauca* and *Colocasia esculenta* with 22 residues different). Ferredoxin is obviously a less conservative protein than cytochrome *c* and it remains to be determined at which taxonomic level comparison of ferredoxin sequences will be useful.

Prospects for the Future.—The prospects for the use of amino acid sequence data in plant phylogeny in the near future are limited. This derives largely from the fact that the real bottleneck in plant protein sequence determination is the isolation and purification of suitable plant proteins for sequencing. Several limiting factors are operative in the selection of a protein for sequencing: size (less than about 15,000 daltons for practical comparisons among numerous taxa), relative ease of purification in milligram quantities, wide taxonomic occurrence, and high cellular concentration. Technical requirements of purification often exclude the taxonomically most interesting species. For example, purification of sufficient cytochrome *c* for a sequence determination requires several hundred pounds of highly viable, rapidly germinating seed, which effectively limits the plants examined to horticultural crops. Automated devices (sequenators) are now commercially available to automatically determine the amino acid sequence of peptides up to 40–50 residues long (subject to certain conditions). These devices will greatly facilitate the determination of sequences, per se, but higher plants are generally poor sources of protein for both biological (low metabolic activity) and technical (resistant cell walls) reasons. Therefore, purification is likely to remain the bottleneck in the use of plant protein sequences in the near future.

CONCLUSION

Before the full impact of utilizing amino acid sequence data in phylogenetic studies among the angiosperms is felt, it will be necessary to have available a much

greater number of sequences from numerous and diverse taxa. Acquisition of these data will require considerable time, work, and a modicum of good luck in identifying and sequencing suitable proteins. Protein sequence data have not and are unlikely to revolutionize presently accepted phylogenetic proposals. The value of protein sequence data in botany, as in zoology, is to provide an independent, objective source of data against which to compare traditional phylogenetic schemes. It is too early to assess the ultimate impact of sequence data on phylogenetic schemes. Indeed, if the discipline of biochemical systematics in general could be said to be approaching puberty (and certainly not yet maturity), the use of plant protein sequences for phylogenetic studies remains in very early infancy.

MACROMOLECULES—NUCLEIC ACID HYBRIDIZATIONS

The technique of nucleic acid hybridization is, in principle, applicable to chemotaxonomy at all taxonomic levels since it involves the fundamental hereditary material deoxyribonucleic acid (DNA) and its transcribed copy, ribonucleic acid (RNA). Following development of techniques for denaturing (or unwinding) the helical DNA of viruses and bacteria and subsequent "hybridizations" of the derived single strands, similar techniques were developed for use with the DNA's of animals and plants. The methods involve the extraction of denatured DNA strands and, most commonly, trapping these single-stranded DNA's on nitrocellulose filters. RNA or fragmented DNA from the same or another organism is used as a test against the long-strand DNA already present in the test system. The low molecular weight nucleic acid (RNA or sheared DNA) has a tendency to pair with the original DNA; the affinity (or extent of pairing) reflects similarity between the two interacting nucleic acids.

In contrast to the relative ease with which meaningful plant natural products distribution patterns are determined are the difficulties and patience required to carry out nucleic acid hybridization experiments and to interpret their results. Thus, it is not surprising that too few nucleic acid hybridization data (see, for example, Bendich & Bolton, 1967; Bendich & McCarthy, 1970) are available for higher plants that bear upon the interpretations of Cronquist and Takhtajan for the evolutionary relationships of angiosperms; nevertheless, the method inherently has great potential. One investigation involving DNA-DNA and DNA-RNA hybridization studies with plants belonging to Centrospermae (Caryophyllales) and related families (Mabry et al., 1972; Chang, 1971 and references therein) can serve to illustrate the technique and its potential. DNA-DNA and DNA-RNA hybridizations were employed for determining the extent of genetic homology among species which belong to various betalain-producing plant families relative to species which are members of anthocyanin-producing families, especially the Caryophyllaceae.

The DNA-DNA hybridization results were somewhat surprising in that only between varieties of the same species (*Beta vulgaris*, the red and sugar beets) was competition detected; that is, no differentiation between genera, let alone higher taxonomic categories was observed.

Next, ribosomal RNA (r-RNA) was used for hybridization with DNA since it is well known that the cistrons for r-RNA are relatively conserved (few

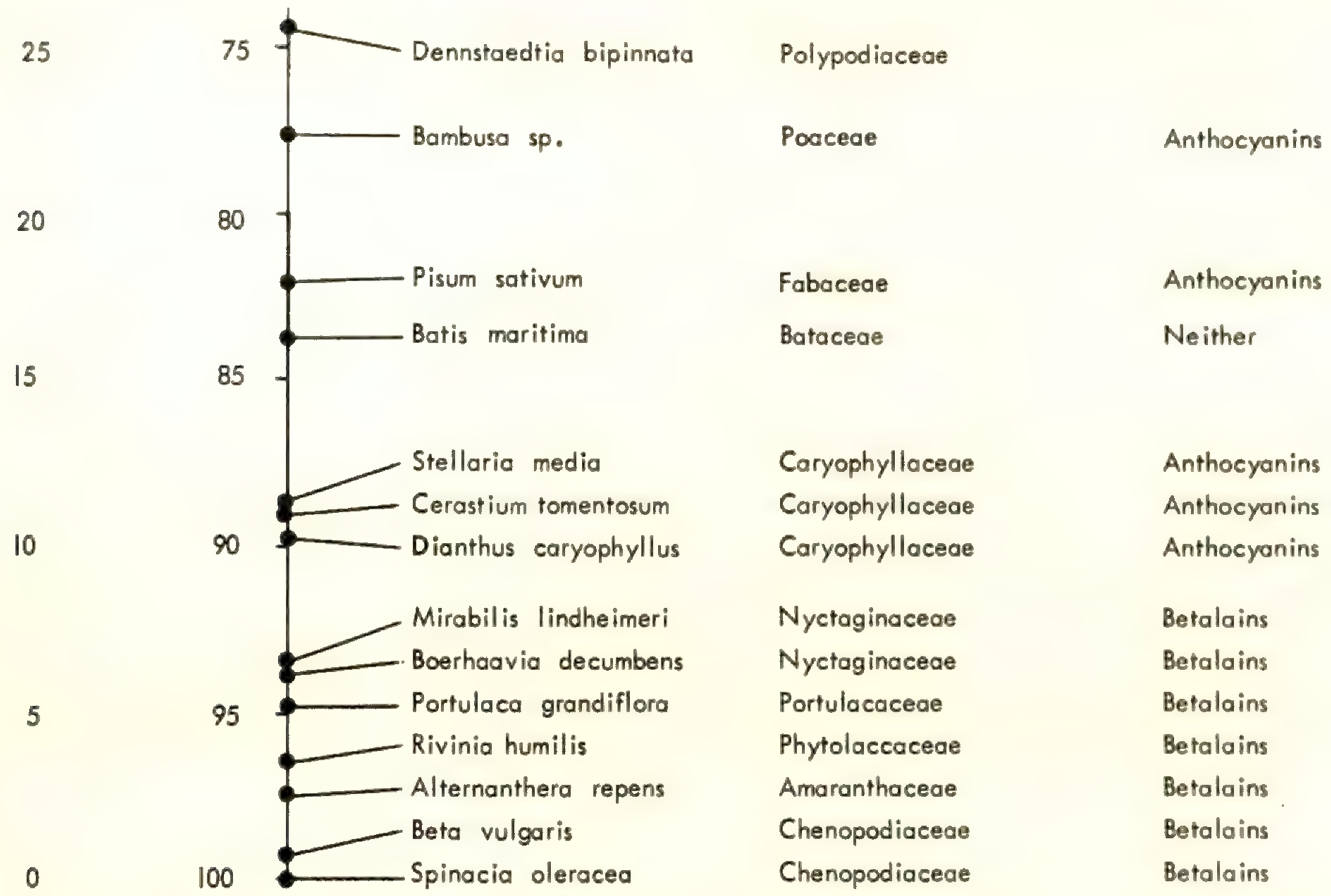

FIGURE 14. 16S r-RNA homologies in plants. In all experiments, 0.6 μg of ^{3}H-spinach 16S r-RNA (4000 cpm/μg) were incubated with 12 μg of spinach DNA bound on a nitrocellulose filter in 0.1 ml of foramide: 4 SSC (1:1) at 40°, in the presence of increasing amounts of r-RNA from other taxa. After 38 hours, each filter was washed with 2 ml of foramide SSC solution for 5 minutes at 40°, then with 2 more ml SSC for another 5 minutes. Each value in this figure represents the average obtained from three determinations. The ratio of labeled r-RNA to DNA in the hybrid in the absence of competitor r-RNA was 0.33%, representing 7% binding of the input labeled r-RNA. All values have been corrected for background binding using calf thymus DNA filters (Chang, 1971).

mutations) compared with the average DNA cistrons. The results obtained by DNA-RNA hybridizations indicated that excess r-RNA from a distantly related yeast (see Chang, 1971) could not inhibit the labeled 16S r-RNA from the betalain-producing spinach (*Spinacia oleracea*, Chenopodiaceae) from hybridizing with the filter-bound DNA from the same plant; on the other hand, excess r-RNA from the still somewhat distantly related pea, *Pisum sativum*, a member of the anthocyanin-producing Fabaceae, did reduce the homologous spinach-r-RNA/spinach-DNA hybridization to about 18% (Fig. 14).

The crucial experiments involved r-RNA from the Caryophyllaceae and from the betalain-producing families. Excess r-RNA from either of three genera (*Dianthus*, *Cerastium*, and *Stellaria*) from the anthocyanin-producing Caryophyllaceae and one species from the Bataceae (neither anthocyanins nor betalains) reduced the spinach r-RNA/spinach-DNA interaction to 10–15% and 17%, respectively. Significantly, however, excess r-RNA from several betalain-producing families reduced the spinach-r-RNA/spinach-DNA hybridization in every case to less than 7% (see Fig. 14). That is, the r-RNA from betalain-producing plants

showed 93.5% or more homology with the r-RNA from the test system, *Spinacia oleraceae* (Chenopodiaceae).

All of the data available (see earlier section II-A on pigments) support a close evolutionary relationship of all the betalain-producing families and indicate that the Caryophyllaceae and Bataceae, although phylogenetically close to, are nevertheless distinct from the betalain-producing families.[12] Although these data do not necessarily discount the interpretations of either Cronquist or Takhtajan with regard to these families, the results are in close agreement with Mabry et al. (1963) and suggest that Cronquist is correct in excluding the Bataceae from his Caryophyllales.

General Summary and Conclusions

As has been stated repeatedly by the present author (Turner, 1967, 1969, 1972), the most convenient way to present and discuss biochemical data as related to systematics is to treat these under the broad headings, macro- or micromolecular approaches. Each of the above authors has presented, in at least brief fashion, *macro*molecular data bearing on angiosperm phylogeny (Fairbrothers, serology; Scogin, primary structure of proteins; Mabry, nucleic acid hybridizations), while Mabry has attempted the almost impossible task of making meaningful the *micro*molecular data (Hegnauer was unable to do this in six volumes!).

MICROMOLECULAR APPROACHES

Over the years more effort in man hours, albeit mostly by chemists, has gone into the accumulation of micromolecular data than in the assemblage of macromolecular data. This has resulted in a large mass of information, a kind of flotsum from the bench of the organic chemist which was swept into the literature following his particular structural interests. Most of the early reports of such molecules (and even many today) were largely undocumented as to plant source, and consequently, many identification errors were incorporated, thus compounding the effort of systematists to organize and "make sense" of these data[13] (cf. the excellent discussion by Ettlinger & Kjaer, 1968).

The only really good recent account of the distribution of micromolecules among flowering plants generally is the six-volume compendium of Hegnauer, and unfortunately for the average American doctorate (including myself), its contents are not easily deciphered, either as to translation or phyletic meaning.

MACROMOLECULAR APPROACHES

Because of its early development, inexpensive and easy application, and relatively comprehensible form of data presentation, the serological approach

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[12] In this connection, it is especially noteworthy that neither the Bataceae, Caryophyllaceae, nor the Molluginaceae contain alkaloids in contrast to most of the betalain-producing families (Raffauf, 1970).

[13] I am reminded especially of Cronquist's (1968: 178) one paragraph digression on a reputed "exception to the mutual antipathy of betalains and anthocyanins" in the Aizoaceae, appropriately referred to by Mabry. The literature is replete with such errors (in this case an artifact of chemical procedure, not identification) and one could keep the hounds at bay a very long time by just digging up this or that erroneous exception to defend a point of view.

has heretofore had the most to offer systematists interested in classification at the familial level or higher. But even here the data are fragmentary and, except for an occasional genus or family, information is mostly missing for the more critical groups.

More perplexing for this reviewer is the fact that at least some serological data are available for the hypothetically "more primitive," woody magnolian lines, but other kinds of macromolecular data (either protein or nucleic acid) are absent for these groups. This is unfortunate since, taken alone, serology has little to offer in the way of evidence bearing on the relative age of a group. Still, as indicated by Fairbrothers, in the case of *Illicium*, *Paeonia*, and numerous other genera among several orders, serological data have been useful in suggesting, in a relative way, cladistic distances among selected families. It would seem unnecessarily repetitive to reiterate here what he has so nicely sketched out for us. I will, therefore, confine any additional "serological comments" to those few instances where the presentations of either Mabry or Scogin seem to warrant such considerations.

Unquestionably, the most remarkable new data which have become available to plant systematists for use at the familial level or higher has been that of cytochrome *c*, mostly coming out of Professor Donald Boulter's laboratory in Durham, England. This work has been placed in proper perspective by Scogin, who recently worked in Dr. Boulter's laboratory as a post-doctoral fellow, helping with the amino acid sequence of cytochrome *c* from tomato.

Because of the *potential* significance of this work in determining the more or less "primitive" groups among angiosperms generally, I think the taxonomic community owes Professor Boulter (who, after all, is a plant physiologist by training) a special accolade. And I can't help but add here a vignette of my own. During 1966–1967 I also worked as a post-doctoral fellow in Dr. Boulter's laboratory (at that time associated with the University of Liverpool), mostly "mucking" around with protein bands and isozymes. I soon became disillusioned with the potential of these data as taxonomic guidelines above the generic level and, being familiar with Margoliash's comparative work on cytochrome *c* among animal groups, strongly urged Don to turn his botanical efforts in this direction. At first he made light of my suggestions, setting up instead, *for my use*, an appropriate column for cytochrome *c* isolation. I failed miserably, but he must have been sufficiently impressed with my dedication and interest (or perhaps partial success?) to take on the task himself. In this vain but humble way, I too feel part of the "cutting edge" (as current terminology would have it) of the phyletic art being practiced today. Now let's look at the data, as sparse as it is.

If, as has been suggested, cytochrome *c* has evolved at a relatively uniform rate over time, then one has a kind of clock with which to calculate the likely divergence of cladistic assemblages. As noted by Scogin, this clock has kept relatively good time in the animal kingdom; at least it jibes with what is known of the fossil record.[14]

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[14] The clock might occasionally run fast (Carlson & Brosemer, 1973), but the exceptions seem open to other interpretations, or at least seem confined to short-term specialized lines.

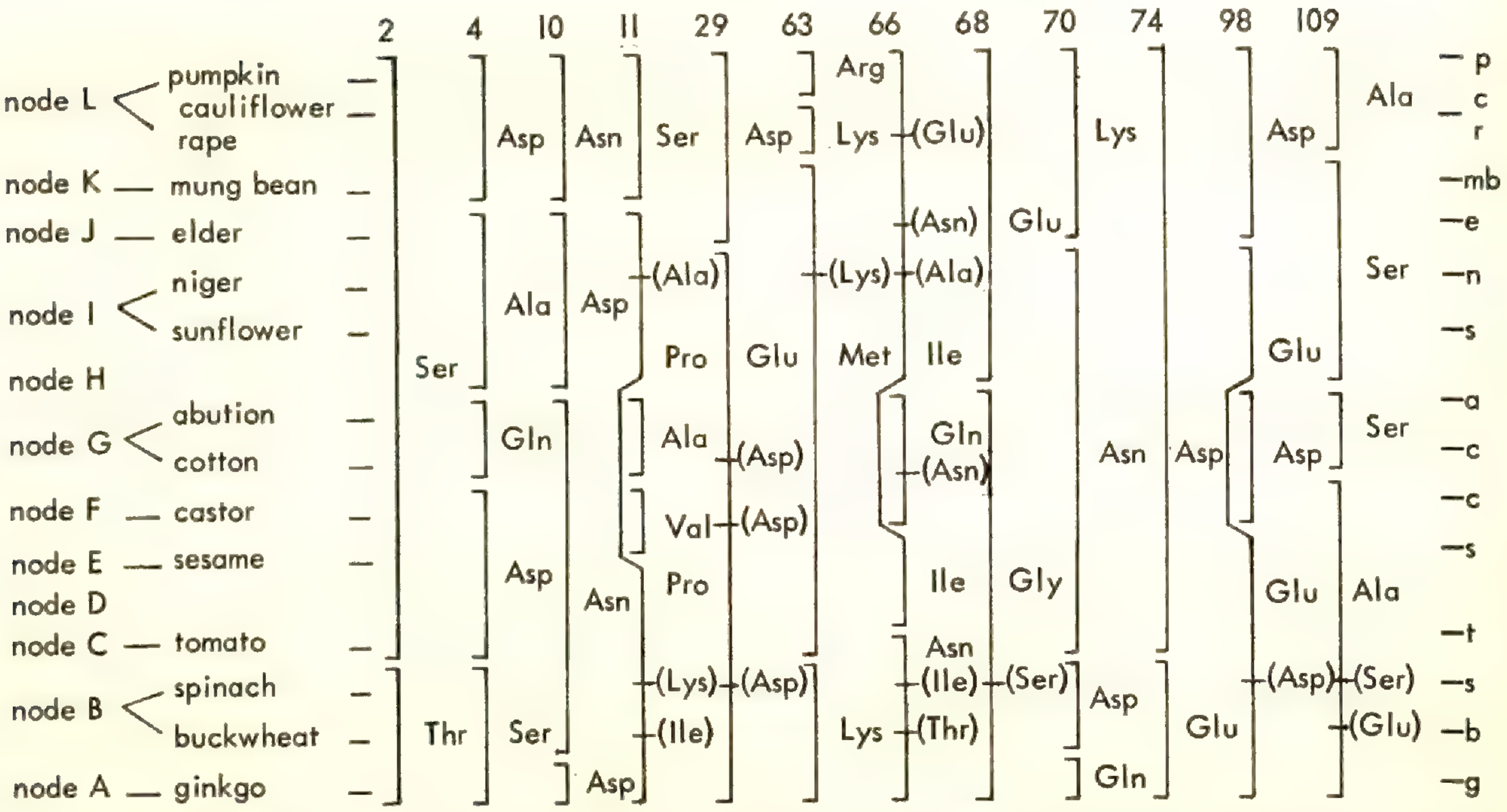

FIGURE 15. Differences between plant cytochromes *c*. Positions where differences in the sequences occur, which lead to differences along the nodal line of descent. The nodal residue for each group of nodes is shown. In cases where a sequence differs from the adjacent node, the amino acid is indicated in brackets. The lettering and topology of the nodes is as given in Fig. 13, and the numbers refer to the positions in the complete sequence (after Boulter et al., 1972).

Has the clock also kept reasonably good time for the plant kingdom, especially among angiosperms? This, of course, we do not know, for there is that abominable fossil gap between the angiosperms and other plant groups somewhere below the Cretaceous. But let's assume that the amino acid ticker for plants runs at about one substitution every 25 million years or so, much as it apparently has for most animals. What can we say then about the relative time of divergence of various plant groups, especially angiosperms, based on the data tabulated to date?

This, in fact, has been done by Ramshaw et al. (1972), using data from approximately 20 species of plants, including 14 dicots distributed among 12 families (Fig. 15) and several monocots. Assuming a monophyletic origin, these data suggest that the angiosperms arose somewhere before the Jurassic, between 400 and 520 million years ago. Further, the data suggest that the monocots were probably derived from the dicots around 230 million years ago, and that of those angiosperms examined to date, the Chenopodiaceae-Polygonaceae line was among the first (about 300–400 million years ago) to diverge from that line leading out of *Ginkgo*, the only truly primitive vascular plant examined by Boulter's group.

Figure 13 in Scogin's paper summarizes much of what is believed to be a "best fit" phyletic tree of the dicots, constructed from one of several, highly sophisticated, computer-programmed approaches (some, if not all, of which have been soundly criticized by Crowson (1972). However scrappy the data, several interesting suggestions emerge:

1. The Chenopodiaceae-Polygonaceae line seems to have branched quite early from the ancestral plexus which gave rise to the angiosperms generally, supporting the contention of Mabry et al. (1963), and perhaps others, that the betalain-

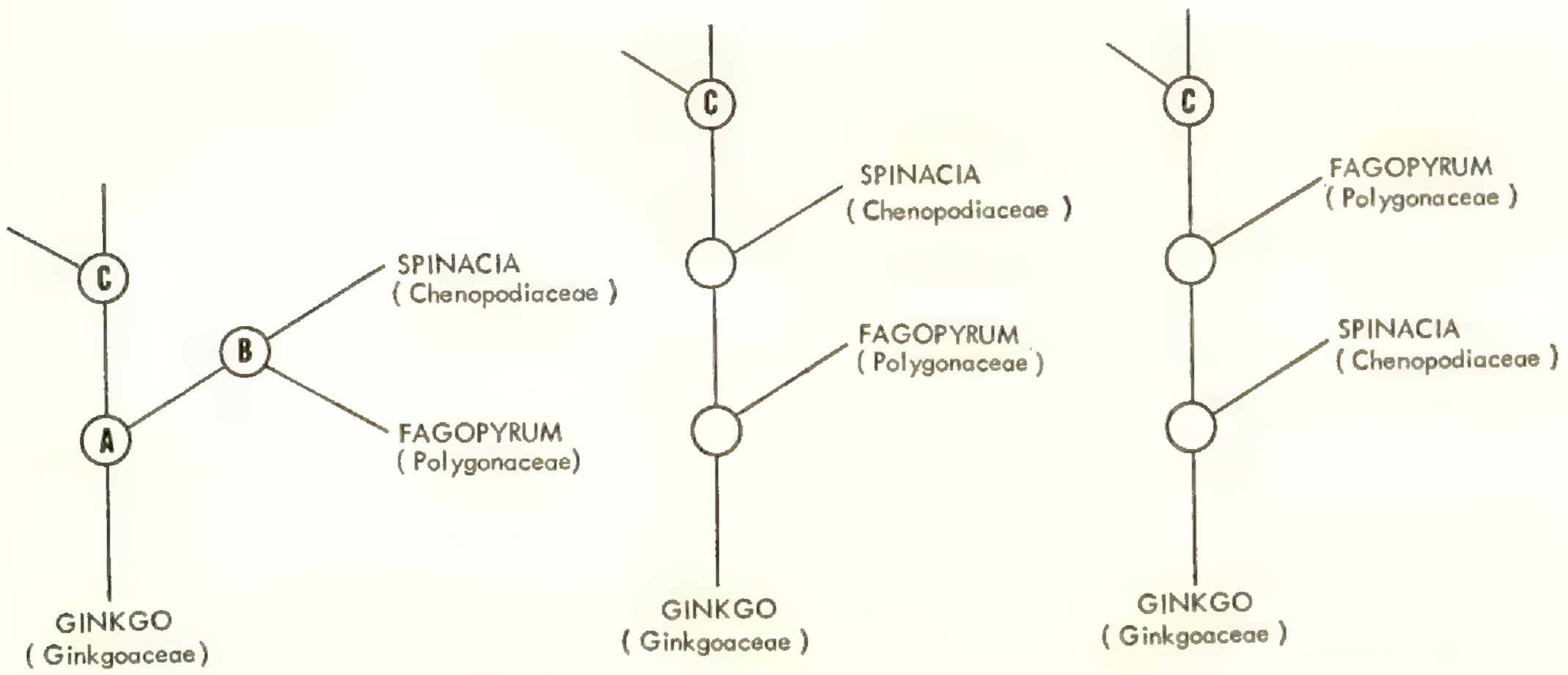

FIGURE 16. A summary of the three minimum amino-acid substitution phylogenetic trees relating 15 plant species constructed using the "ancestral sequence" method. Node C and the remaining unshown topology is common to all three trees, and is shown in Fig. 13.

containing families largely developed before anthocyanins were developed in the angiosperms generally. And I would add that the eight (!) amino acids separating *Spinicia* from *Fagopyrom* (Fig. 15) suggest that the Polygonaceae is an old line arising out of relatives close to, *but not in*, the betalain-containing complex. In this, I would subscribe to Boulter et al.'s (1972) phyletic arrangement shown in Fig. 16, this being one of several possible, computer-derived, branches of the tree at this particular level. Unfortunately, as already indicated, data of this type are unavailable for the woody, presumably ancient, groups belonging to the Magnoliatae, but it would not be surprising to find that this subclass arose close to, *or even after*, the betalain-containing groups, or Node A on the phyletic tree shown in Fig. 13.

2. Only two amino acids separate the Cucurbitaceae from the Brassicaceae. Ridiculous? Morphologically speaking, of course, for who among us would reckon these two families to be less closely related, either phenetically or cladistically, than the two genera of Asteraceae discussed below? Too little is known at present, but hopefully new sequences among these groups will make us better believers, or disbelievers.

3. Cytochrome *c* from *Helianthus* and *Guizotia*, both members of the tribe Heliantheae of the Asteraceae, differs by three amino acids, *suggesting* that the two genera parted ways perhaps 60 or more million years ago, *suggesting* that the subtribe Coreopsidinae (to which *Guizotia* belongs) is quite remote from the subtribe Heliantheae, *suggesting* that, perhaps, the large family Asteraceae is very old, indeed, with lineal branches back to rather remote ancestral groups, such as the Magnoliatae, which, as Mabry points out, contains some of the same kinds of sesquiterpene lactones as the Asteraceae.

The nucleic acid hybridization data presented by Dr. Mabry is interesting, but clearly the results hardly justify the difficult and complex methodology which one must master before meaningful data can be obtained. The results to date suggest that the betalain families are more closely related one to another

than they are to yet other groups. In fact, the results are so tenuously expressed (Chang, 1971) that one must wince at the prospect of adding yet additional families to the list of families already examined *if* the percent homology shown in Mabry's Fig. 14 is reasonably correct. Unfortunately, the DNA hybridization technique, which held such promise in the beginning, has simply failed to live up to expectations, at least for the moment. Like an iceberg, most of its body must lie somewhere below the surface.

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THE BASES OF ANGIOSPERM PHYLOGENY: PALEOBOTANY[1]

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ABSTRACT

Analysis of certain fossils that have been used as evidence for a pre-Cretaceous origin and diversification of the angiosperms indicates that these fossils are non-angiospermous. A review of the sequential development of morphological features exhibited by Early Cretaceous pollen and leaves indicates that the initial radiation of the angiosperms was occurring at that time. The monocotyledons and dicotyledons diverged early before either class attained a moderate degree of diversity. Subclass Magnoliidae has retained the morphological grade exhibited by the earliest dicotyledonous pollen and leaves. The next youngest grade of Early Cretaceous pollen is found in putatively primitive members of Hamamelididae and Ranunculidae. Stratigraphic series of Early Cretaceous foliage indicate a transition from the morphological grade of Magnoliales to leaf morphology characteristic of Rosidae. Late Cretaceous wood assemblages are characterized by a preponderance of anatomical features that have been previously postulated as primitive and typically lack features thought to be advanced.

Twenty years ago, the inclusion of paleobotany in a symposium of this nature would have been little more than a token gesture. The then prevalent concept was that by the Cretaceous—the time of their first entry in significant numbers in the fossil record—the angiosperms were well diversified into extant orders and families, and even genera (Axelrod, 1970). The diversification having taken place in some area remote from basins of deposition and fossilization (e.g., tropical uplands or Malesia), paleobotany would provide almost no evidence bearing on the phyletic relationships between major angiosperm groupings.

During the last twenty years, however, a growing body of evidence has indicated that the angiosperms were undergoing their major evolutionary radiation during the Cretaceous (Fig. 1). The lack of any definite angiosperm pollen in a great array of pre-Cretaceous samples led Scott et al. (1960) and Hughes (1961) to question the supposed great antiquity of angiosperm diversification. More significantly, palynological work on Cretaceous sequences has uniformly shown that, from the level of the first known and morphologically simple angiosperm pollen types, successively younger horizons yield successively more complex and

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diverse arrays of pollen (Doyle, 1969a; Muller, 1970). Although Early Cretaceous angiosperm leaves have typically been matched with leaves of extant genera and families, renewed interest in foliar morphology of both extant and fossil angiosperms has indicated that Early Cretaceous sequences of angiosperm leaves also display the attainment of increasingly higher levels of specialization (Doyle & Hickey, 1972; Hickey & Doyle, 1972), and that many of these earliest leaves represent the same morphological grade as putatively primitive extant angiosperms (Wolfe, 1972).

We thus consider that paleobotany can contribute to an understanding of phyletic relationships between major angiosperm groups. The overwhelming bulk of angiosperm fossils, of course, represent organs that have not been the primary basis of angiosperm classification and speculation on phylogenetic relationships, that is, much of angiosperm history must be deciphered from interpretations of pollen, leaves, and wood rather than flowers. Basic to such interpretations are the correlations that can be made between morphological specializations in these organs and taxonomic position in systems of classification. As papers presented in this symposium indicate (Hickey & Wolfe; Walker & Doyle), such correlations can be made. Moreover, as classifications become more broadly based on all aspects of the plant, such classifications will be easier to evaluate by means of paleobotanical evidence.

Paleobotanists can approach this problem of correlation of morphological specialization with taxonomic position in two basically dissimilar ways. The first is to attempt to find, for each given fossil, a modern plant that is morphologically similar. If, however, the significance of the observed similarities as indicators of phylogenetic relationships of the modern plant is not understood, then we clearly could be analogizing. Until recently, almost all work on angiosperm fossils used such an approach. If meticulously carried out, such an approach will perhaps give some idea as to the oldest occurrence of a given extant genus and low-level suprageneric groupings, but this approach is basically incapable, as Stebbins (1950) pointed out years ago, of recognizing extinct groups intermediate between various major groups represented in the extant flora.

The second approach to paleobotany can be initially independent of comparisons of fossils with extant plants. In given stratigraphic sequences evolutionary series can be postulated, based on a trend from one morphological type to another. This trend in a time dimension allows us to infer which morphological type is ancestral (oldest) and which is derived (youngest). If such character phylogenies are integrated with the comparative morphological data from extant angiosperms, then we are in a position to evaluate systems of classification that have attempted to incorporate concepts of phylogeny. We are also capable of recognizing which fossils represent extinct intermediates and even fossils that represent distinct evolutionary branches that have failed to survive.

Paleobotany, moreover, is a prime tool in uncovering convergences and hence determining whether groups are mono- or polyphyletic. If a particular character or set of characters in a given organ can be demonstrated to have evolved in more than one temporal-morphological series, then clearly two taxa that possess that character or character set are not necessarily phylogenetically related. If a

particular character can be shown to have evolved in only one series, then extant plants possessing that character compose a monophyletic group or clade.

Evidence on Pre-Cretaceous Diversification

A widely held concept, as we stated previously, is that the angiosperms originated in the early Mesozoic or even late Paleozoic and, by the time they entered the fossil record in significant numbers in the Aptian-Albian interval, had undergone their basic diversification into various extant orders and even families (e.g., Axelrod, 1970). Cited as proof for this concept are various early putative angiosperms. It is pointless to discuss certain of these occurrences; some of them, such as the leaves called *Ungeria* and *Propalmophyllum*, are so poorly preserved that groups such as the ferns or gymnosperms could be represented. Other occurrences of early angiosperms, such as the putatively Jurassic palm wood and roots from Utah (Tidwell et al., 1970), have proven to be almost certainly of Tertiary age (Scott et al., 1972). Still other occurrences, such as the pollen called *Eucommiidites*, have been demonstrated to be gymnospermous rather than angiospermous (Hughes, 1961). Read & Hickey (1972) have shown that *Sanmiguelia*, a palm-like Triassic leaf, lacks features definitive of the palms, and Doyle (1973) has further demonstrated that *Sanmiguelia* lacks diagnostic features of the monocotyledons as a whole.

We will discuss two other examples: the late Triassic leaf called *Furcula* and the Hauterivian fructification called *Onoana*. These two examples, we think, illustrate various problems relative to the taxonomic placement of fossils.

Harris (1932), the describer of the leaf *Furcula*, suggested a possible angiospermous affinity based on the character of the stomatal apparatus and the reticulate or net venation. The stomatal apparatus is indeed the syndetocheilic type that is of wide occurrence in the angiosperms, but in itself is an insufficient basis for assignment to the angiosperms because the same type also occurs in gymnosperms such as the Cycadeoidales and Gnetales. Investigators have, however, overlooked one critical feature of the net venation of *Furcula*. In the woody dicotyledons, with which *Furcula* is compared, the secondary venation is a fundamentally closed type; the closure is most typically accomplished by the looping of the secondary veins, but is also in some instances accomplished by strong branches of the secondary veins or by a marginal vein. Harris noted, however, that in *Furcula* the secondary veins and branches ended blindly at the margin of the lamina and that a continuous marginal vein was lacking; this is a decidedly non-dicotyledonous characteristic and basically represents a modified open venation system. Further, Harris noted that *Furcula* had another feature commonly found in pteridospermous gymnosperms, a bifurcating lamina. Although it is possible that *Furcula* represents some gymnospermous sister-group to the angiosperms, it clearly is not angiospermous.

The oldest fossil interpreted as an angiospermous fruit is *Onoana* from the Hauterivian of California (Chandler & Axelrod, 1961); this fructification thus predates the first occurrence of any other angiospermous organ. *Onoana*, however, does not display any characteristics confined to the angiosperms, that is, it cannot be determined whether *Onoana* is a seed or a fruit; the angiospermous affinity

rests entirely on picture-matching comparisons to fruits of Icacinaceae, particularly the extinct genus *Stizocarya*. In Icacinaceae, the endocarp is pierced partially by canals and is typically formed of interdigitating cells lacking definite orientation; when present, an inner layer is composed typically of interlocking cells, and, in the instance of *Stizocarya*, these cells are star-shaped (Reid & Chandler, 1933). Although *Onoana* has canals in what is interpreted as the endocarp, this layer is formed of apparently parenchymatous cells that are radially aligned; the inner layer in *Onoana* is formed of transversely aligned cells. Thus, the layers that are supposedly homologous between *Onoana* and Icacinaceae are in *Onoana* atypical for Icacinaceae. Added to this is the fact that pitted Icacinaceae have canals that are oriented radially, but in *Onoana* the canals range from radially to obliquely oriented. Thus, in several features, *Onoana* differs from typical icacinaceous fruits; if the relationship to Icacinaceae is problematic, then so is the relationship to the angiosperms because the latter relationship is based on the former. We consider it equally plausible that the inner layer of *Onoana* is homologous with the typically collapsed fleshy inner integumentary layer of gymnosperms and that the supposedly parenchymatous layer may in fact be sclerenchymatous as in gymnosperms, which is indicated by the presence of some fibers near the outer part of this layer. Clearly, it has not been established whether *Onoana* is angiospermous or gymnospermous, but the lack of definitive angiospermous features makes it an insecure basis for inferring the time of diversification of the angiosperms.

Even less secure is the determination of the modern icacinaceous genus *Phytocrene* from Cenomanian or Turonian beds of New York. The object attributed to this genus by Scott & Barghoorn (1957) is apparently not anatomically preserved, and the determination rests solely on the presence of external pits in the fossils. Reid & Chandler (1933: 322) noted that all endocarps of extant Icacinaceae are bisymmetric but the New York specimens are, at best, irregularly bisymmetric to subtriangular. We do not think that sufficient evidence has been presented to substantiate the determination of the New York material as Icacinaceae or even as angiospermous.

We thus consider that there is no unequivocal evidence that indicates a pre-Cretaceous origin for the angiosperms. The supposed diversity of early angiosperm leaf floras is, as discussed elsewhere (Wolfe, 1973), a logical artifact of attempting to match fossil and modern leaves without any concept as to the phyletic and taxonomic significance of various similarities and dissimilarities. As we argue below, the known fossil record of Cretaceous angiosperms can best be interpreted to indicate that the angiosperms were undergoing diversification at major taxonomic levels and that continuing investigations of Cretaceous angiosperm fossils will provide many answers to phylogenetic problems.

THE CRETACEOUS RECORD

POLLEN

One of the most intensively studied Cretaceous sections bearing on the early stages of angiosperm evolution consists of the Potomac Group and Raritan Formation of the Atlantic Coastal Plain (Brenner, 1963, 1967; Doyle, 1969a,

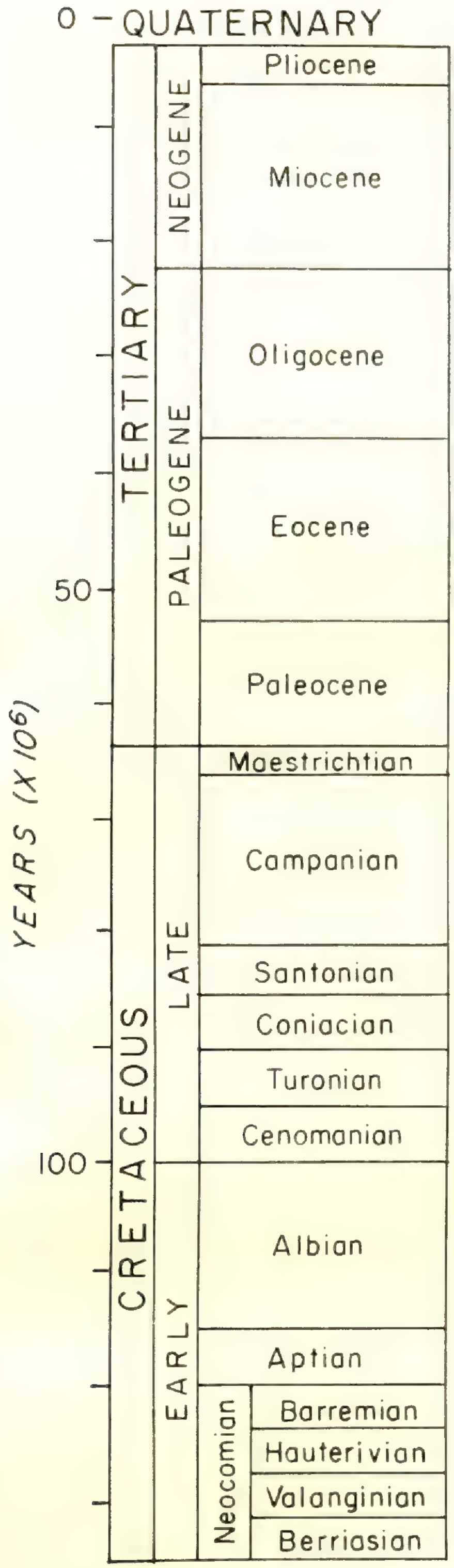


FIGURE 1. Approximate duration of Cretaceous stages and Tertiary epochs (from Wolfe, 1973).

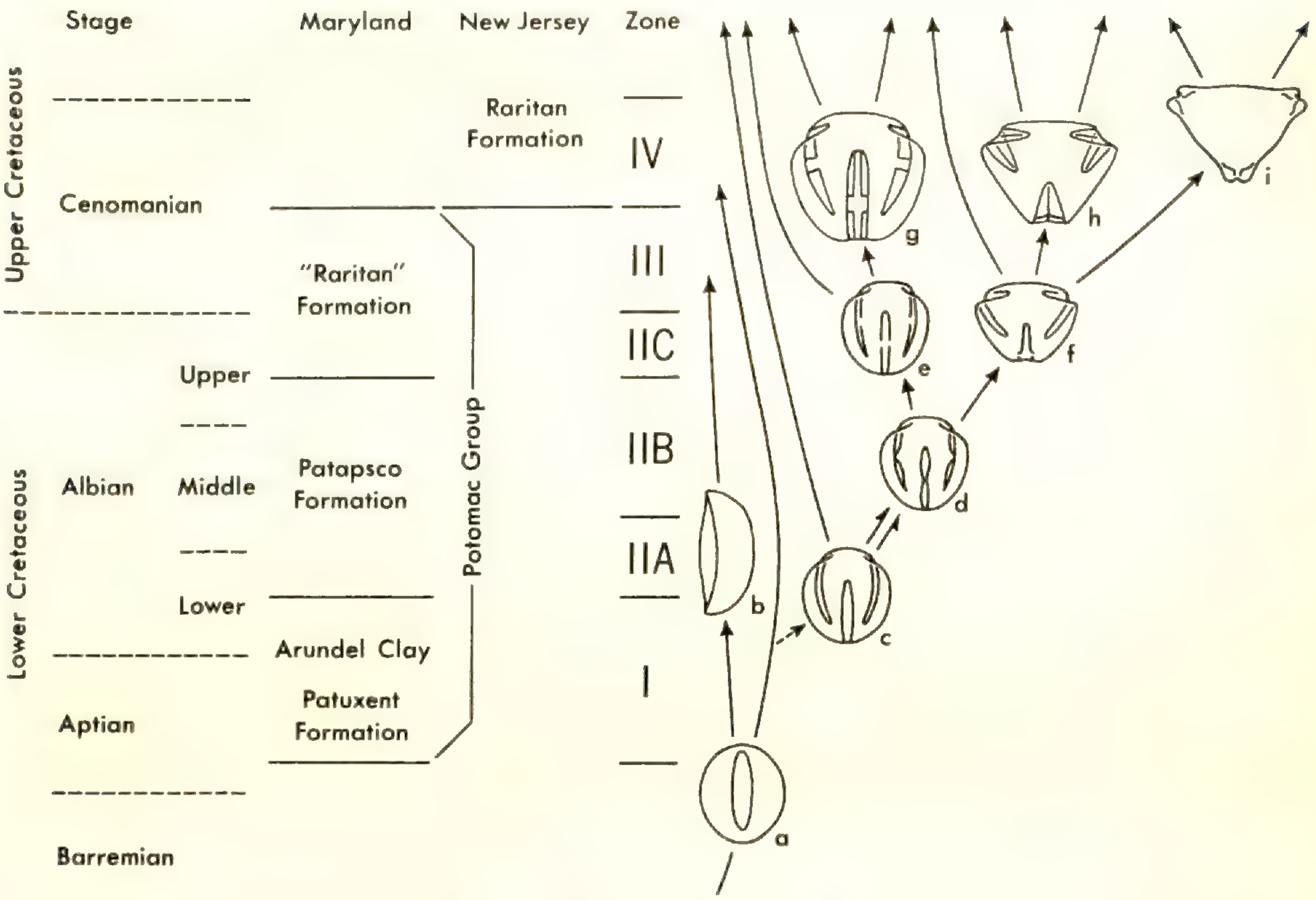


FIGURE 2. Stratigraphic subdivisions of the Atlantic Coastal Plain mid-Cretaceous section, and stratigraphic distribution and presumed evolutionary relationships of major angiosperm pollen types (modified from Doyle, 1973). Suggested correlations of the Maryland and New Jersey lithological units (formations) with the standard European stage sequence are indicated to the left; informal biostratigraphic units or pollen zones (Brenner, 1963; Doyle, 1969b, 1973; Doyle & Hickey, 1972) are indicated by roman numerals in the middle. Pollen types indicated to the right are: (a) generalized tectate-columellate angiospermous monosulcates (*Clavatipollenites*, *Retimonocolpites* spp.); (b) monocotyledonoid reticulate monosulcates (*Liliacidites* spp.); (c) generally reticulate-tectate tricolpates (non-magnoliid dicotyledons: *Tricolpites* spp.); (d) generally reticulate-tectate tricolporoidates (*Tricolpites*, *Tricolporoidites* spp.); (e) small, generally smooth-walled, prolate tricolporoidates (*Tricolporoidites* spp.); (f) small, generally smooth-walled, oblate-triangular tricolporoidates (*Tricolporoidites*, *Pericipollis* spp.); (g) larger, often more highly sculptured, prolate tricolpor(oid)ates (*Tricolporoidites*, *Tricolporopollenites* spp.); (h) larger, often more highly sculptured, oblate-triangular tricolpor(oid)ates (*Tricolporoidites*, *Tricolporopollenites* spp.); (i) primitive members of the triporate Normapolles complex (*Complexiopollis*, *Atlantopollis* spp.). Arrows indicate modes of origin, not necessarily individual evolutionary lines. The dashed arrow indicates the uncertain mode of origin of tricolpates; the double arrow emphasizes the multiple origin of tricolporoidates from tricolpates.

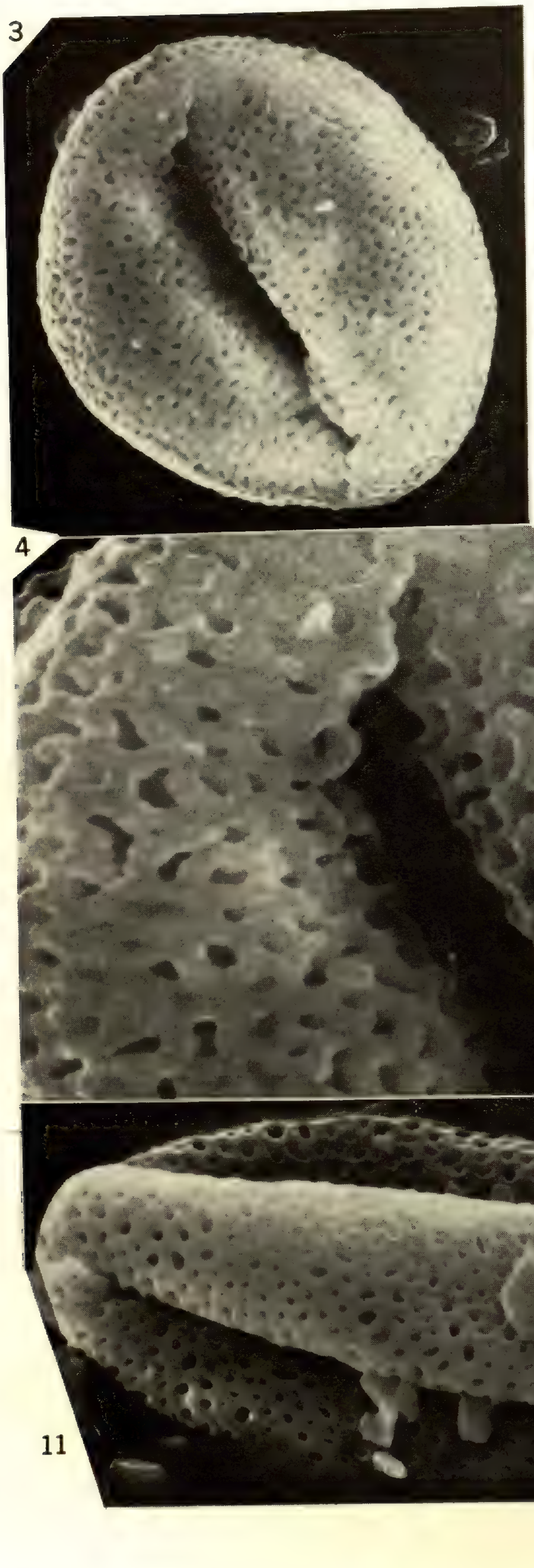
1969b, 1970, 1973; Wolfe & Pakiser, 1971). Although only the middle part of the Raritan Formation is dated directly by marine fossils, close similarities with pollen and leaf floras of other areas which have been dated independently allow detailed correlations with the standard European stage sequence (Fig. 1; cf. Brenner, 1963; Kemp, 1968, 1970; Norris, 1967; Hedlund & Norris, 1968; Doyle, 1969a, 1969b; Doyle & Hickey, 1972, in press; Wolfe & Pakiser, 1971; Pacltová, 1971). These comparisons also indicate that the pattern of diversification of pollen types seen in the Potomac-Raritan section (summarized on right side of Fig. 2) is sufficiently consistent with changes occurring elsewhere in the world to serve

as a basis for conclusions on general questions of angiosperm phylogeny (Doyle, 1969a; Muller, 1970; Doyle & Hickey, in press).

The only angiospermous pollen grains in the lowest part of the Potomac Group (the lower half of Zone I of Brenner, 1963: Aptian?) are very subordinate monosulcate forms, with a single polar germination furrow, generally assigned to the form genera *Clavatipollenites*, *Retimonocolpites*, and *Liliacidites* (Figs. 3–9; cf. Brenner, 1963; Doyle, 1969a, 1970, 1973). Although monosulcate pollen also occurs in several groups of gymnosperms (e.g., Cycadales, Ginkgoales, Bennettitales), the above three genera have a wall or exine which is tectate and columellate, that is, consisting of an inner and outer layer (nexine and tectum) connected by a layer of well-defined rods or columellae (compare light and scanning electron micrographs of *Clavatipollenites*: Figs. 3–7), which is a character restricted to the angiosperms (Van Campo, 1971). Present SEM and light microscopic data indicate that exine structure of *Clavatipollenites* is tectate-perforate rather than clavate, as originally believed. This invalidates the "pilate or retipilate to reticulate or completely tegillate" trend postulated by Doyle (1969a: 28) and is more consistent with the tectate to semitectate to intectate trend of Walker (1974; Walker & Doyle, this symposium). *Clavatipollenites* (*C. hughesii*) was first described from presumably older (Barremian) rocks of England (Couper, 1958; Kemp, 1968), making it the oldest definite angiosperm pollen type known. Jurassic grains assigned to *Clavatipollenites* (cited by Muller, 1970) appear to have cycad-like alveolar exine structure and are hence not angiospermous. By early Potomac time, angiospermous monosulcates had already achieved some diversity, including larger, more coarsely reticulate, and suggestively monocotyledonoid forms (*Liliacidites*, with finer sculpture restricted to the ends of the grains and sulcus margins: Figs. 8–9; included in *Retimonocolpites* by Doyle, 1973).

In the upper part of Brenner's Zone I (lower Albian?), the monosulcates are joined by rare tectate-columellate tricolpate grains, with three longitudinal furrows or colpi (Figs. 11–13). Presumably somewhat older tricolpates are reported from Aptian rocks of Brazil (Müller, 1966), Africa (Jardiné & Magloire, 1965; Doyle, Jardiné & Doerenkamp, unpublished), and Israel (Brenner, in press). Although no actual transition is known, similarities in size and exine structure (compare Figs. 3–7 and 11–13) suggest that the earliest tricolpates were derived from the *Clavatipollenites-Retimonocolpites* complex. One of several hypotheses for the mode of origin of tricolpate pollen proposes that first the single polar furrow of monosulcate pollen developed into a three-armed structure (trichotomosulcate), and subsequently the central (polar) part of the furrow was eliminated, stranding the three arms as equatorially located colpi (Straka, 1963; Wilson, 1964). Though too young to be the actual intermediates, trichotomosulcate and irregularly colpate variants of *Clavatipollenites* are known from middle Zone II in the Potomac sequence (Fig. 10; Doyle, 1969a) and the middle Albian of Oklahoma (Hedlund & Norris, 1968).

Late Zone I and early Zone II tricolpates are relatively uniform in size, shape, and exine structure—small to medium-sized, prolate, and tectate to semitectate (reticulate)—but in the course of Zone II and Zone III (middle Albian through



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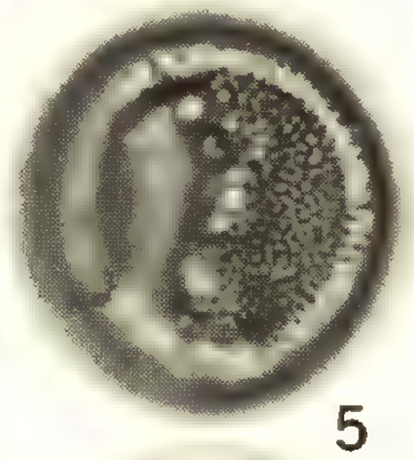

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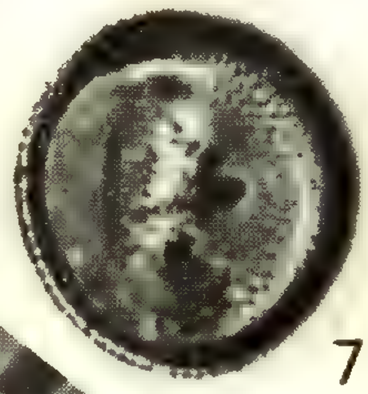

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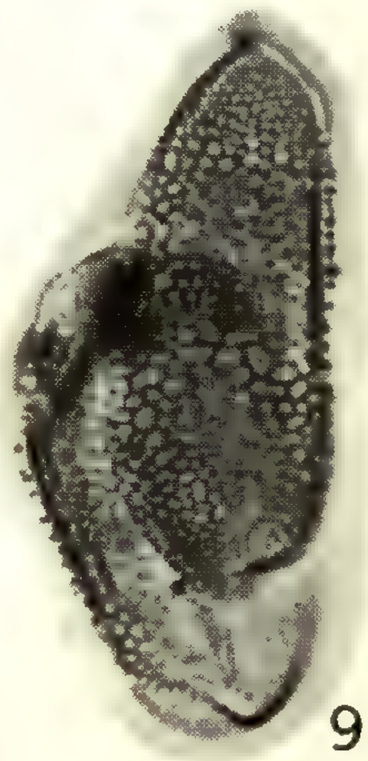

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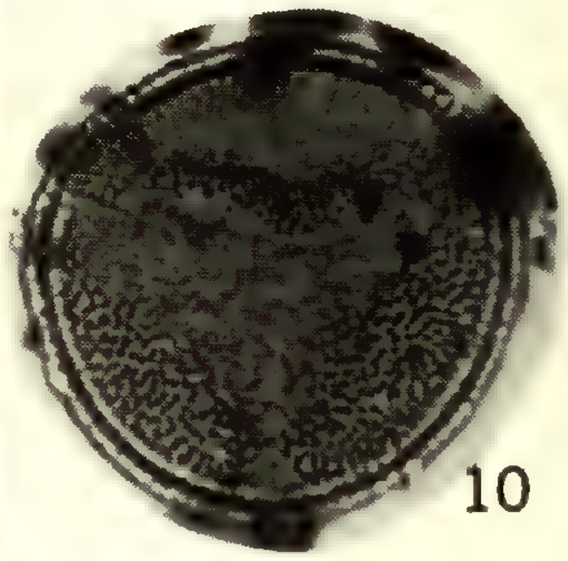

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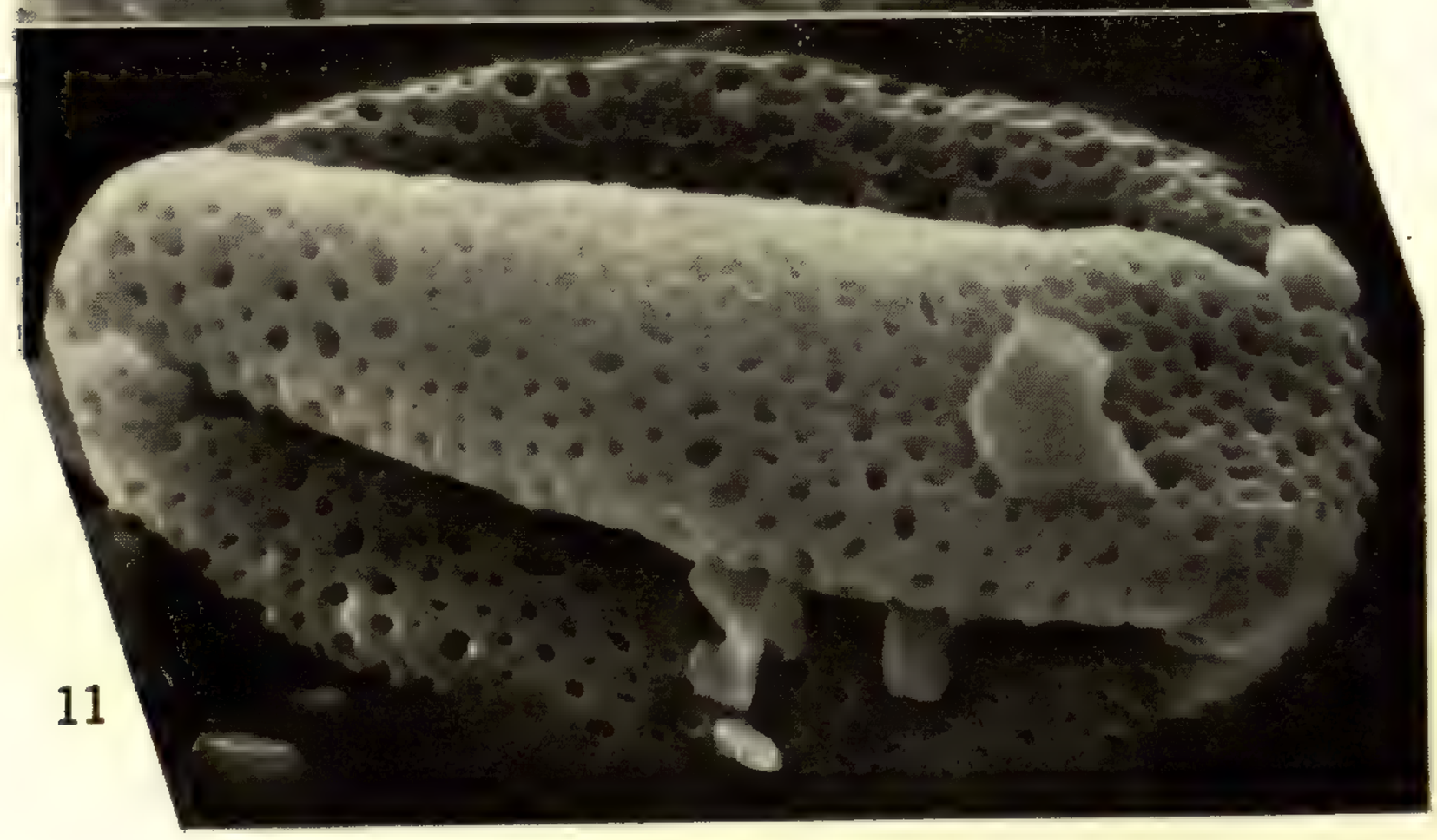

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lower Cenomanian?) they undergo various independent and divergent modifications. Some of these involve size and sculpture, resulting in very large (Figs. 14–15), very small (Figs. 23–29), smooth-walled (Figs. 21–22), and coarsely sculptured, sometimes rugulate-reticulate grains (Figs. 16–20). Interestingly, many of the same trends are seen among contemporaneous monosulcates. A more significant trend, involving only the tricolpates, is the thinning of the colpus membranes and margins at the equator, culminating by Zone III times (lower Cenomanian?) in distinct ora associated with the colpi—the tricolporate condition (Figs. 25–40). Significantly, this trend apparently occurred independently in several tricolpate lines (as characterized on size and sculpture), although it is most common in the smaller and smoother lineages and is often correlated with a change in shape to oblate and triangular in polar view, with the apertures at the protruding corners of the grains (Figs. 37–42). Within Zone III and Zone IV (middle Cenomanian?), many of the tricolporates show a secondary tendency to increase in size and elaboration of exine structure and colpus margins (Figs. 33–43), a trend also inferred from comparative studies of modern tricolporate groups (Van Campo, 1966; Dahl, 1952). In at least one triangular tricolporate lineage, the shape modification trend is correlated with shortening of the colpi, leading to their elimination in the first triporate grains of Zone IV (Figs. 44–45). These grains represent early members of the Normapolles complex, a group which flourished during the Late Cretaceous in eastern North America and Europe (Góczán et al., 1967; Wolfe & Pakiser, 1971; Doyle, 1969a).

The evolutionary trends evidenced in the pollen of the Potomac-Raritan sequence and its equivalents have obvious phylogenetic implications if the successive transformations and grades of advancement are correlated with the distribution of characters in the modern flora. Here it is important to bear in mind that we are *not* using the systematic distribution of characters to establish first records of modern groups, but rather using the fossil record to draw con-

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FIGURES 3–13. Potomac Group (Cretaceous) angiosperm pollen: monosulcates and earliest tricolpates. All figures 1000× unless otherwise indicated; coordinates: UMMP Zeiss RA microscope # 4767359.—3–7. *Clavatipollenites* cf. *hughesii* Couper, 1958.—3. Lower Zone I (Aptian?). Angiospermous tectate-columellate monosulcate, scanning electron micrograph; ca. 4000×. Note well-developed tectum with numerous perforations. Sample Aq 27 (see Doyle, 1969a: 33).—4. Ca. 12,000×. Note occasional columellae visible through tectal perforations.—5–7. Light micrographs, three focal levels. Columellae appear as black dots at higher focal levels, radially oriented rods in optical section. Slide Aq 27-11, coordinates 7.4 × 85.2.—8–9. *Liliacidites* sp. (= *Retimonocolpites* sp. C, sensu Doyle, 1973), lower Zone I (Aptian?). Monocotyledonoid monosulcate, two grains, two focal levels. Note differentiation of the reticulate sculpture into finer and coarser areas (ends, middle of grain respectively). 71-8-1d (Trent's Reach, Va.: preparation from USNM 3215), coordinates 7.6 × 89.0.—10. Cf. *Asteropollis asteroides* Hedlund & Norris, 1968; middle Subzone II-B (upper middle Albian?). Trichotomosulcate variant of the *Clavatipollenites* complex. D12-520-2b (Delaware City well D12: Delaware Geological Survey well # Dc 53-7), coordinates 8.3 × 93.2.—11–13. Aff. *"Tricolpopollenites" crassimurus* Groot & Penny, 1960.—11. Upper Zone 1 (Aptian-lower Albian?). One of the oldest Potomac reticulate-tectate tricolpates (non-magnoliid dicotyledons), scanning electron micrograph; ca. 4000×. Note similarity of the tectate-perforate to reticulate sculpture to that seen in *Clavatipollenites* (Figs. 3–4). Sample 69-21 (Arundel Clay, United Clay Mine, near Poplar, Md.: Station 6 of Brenner, 1963).—12–13. Light micrographs, two focal levels. Note reticulate sculpture, columellae. 69-21-1a, coordinates 9.9 × 90.3.

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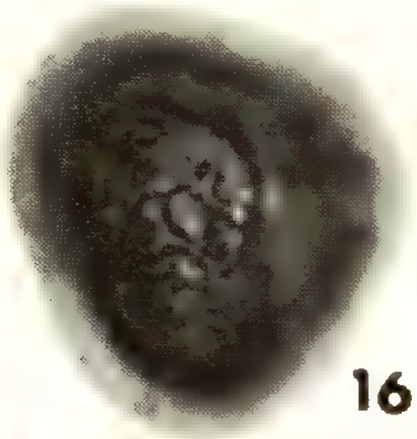
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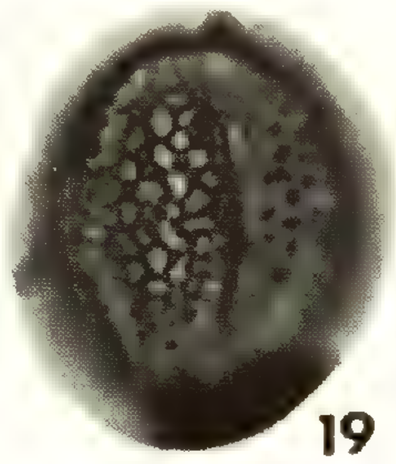
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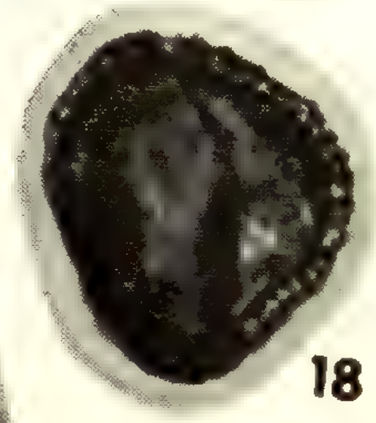
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clusions on the relative advancement of modern groups (or actually their most primitive members) and to evaluate proposed relationships between them. The first appearance of particular pollen types represent only *maximum* presently allowable ages of the modern groups that retain them; the vast majority of mid-Cretaceous pollen types are probably distant common ancestors of the various groups cited or extinct early side branches with no direct modern descendants, and not plants that could be assigned to modern families, orders, or even subclasses.

First, the oldest and presumably primitive monosulcate pollen type (as in *Clavatipollenites*, *Retimonocolpites*, and *Liliacidites*) is now restricted to the

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FIGURES 14–45. Potomac-Raritan (Cretaceous) angiosperm pollen, illustrating trends within the triaperturate complex. All figures 1000×; coordinates: UMMP Zeiss RA microscope # 4767359.—14–15. *"Retitricolpites" geranioides* (Couper) sensu Brenner, 1963; upper Subzone II-B (lower upper Albian?). Reticulate tricolpate, two focal levels. Note large size, coarse columellae. Slide D13-540-1b (Delaware City well D13: Delaware Geological Survey well # Ec 14-1), coordinates 18.2 × 92.3.—16–18. *"Retitricolpites" vermimurus* Brenner, 1963; middle Subzone II-B (upper middle Albian?). Rugulate-reticulate tricolpate, three focal levels. Note coarse rugulate-reticulate sculpture. D12-515-1c, coordinates 13.0 × 91.7.—19–20. Cf. *"Retitricolpites" georgensis* Brenner, 1963; middle Subzone II-B (upper middle Albian?). Reticulate tricolpate, two focal levels. Note coarse reticulate sculpture, especially in the mesocolpial areas. D12-590-1b, coordinates 7.1 × 92.5.—21–22. *Tricolpites* cf. *albiensis* Kemp, 1968; middle Subzone II-B (upper middle Albian?). Tectate-psilate(?) tricolpate, two focal levels. Note very fine structure and nearly smooth exine. D12-515-1d, coordinates, 13.5 × 99.4.—23–24. Aff. *"Tricolpopollenites" micromunus* Groot & Penny, 1960; Subzone II-A (lower middle Albian?). Reticulate tricolpate, two focal levels. Note small size, reticulate sculpture; compare with Figs. 25–27. D13-725-1a, coordinates 8.9 × 91.3.—25–27. Aff. *"Tricolpopollenites" micromunus*, middle Subzone II-B (upper middle Albian?). Reticulate tricolporoidate, three focal levels. Compare with Figs. 23–24; note buckling-out of centers of the colpi. D13-600-1a, coordinates 5.3 × 99.5.—28–29. *"Tricolpopollenites" minutus* Brenner, 1963; upper Subzone II-B (lower upper Albian?). Reticulate tricolporoidate, two focal levels. Note very small size, fine reticulate sculpture. D13-555-1b, coordinates 8.3 × 98.6.—30–32. Cf. *"Tricolporopollenites" distinctus* Groot & Penny, 1960; Subzone II-C (uppermost Albian-basal Cenomanian?). Psilate tricolporoidate, three focal levels. Compare with Figs. 21–22; note small size, smooth exine, and oroid thin areas at the centers of the colpi. D13-420-1c, coordinates 9.7 × 97.7.—33–34. *Tricolporodites* aff. *bohemicus* Pacltová, 1971; lower Zone III (lower Cenomanian?). Reticulate tricolporoidate, two focal levels. Compare with Figs. 35–36, 43. D12-275-1a, coordinates 3.2 × 94.9.—35–36. *Tricolporopollenites* sp. A, upper Zone III (upper lower Cenomanian?). Reticulate tricolporate, two focal levels. Compare Figs. 33–34, 43; note larger size, more elaborated colpus margins than in Figs. 33–34. D13-215-1b, coordinates 15.4 × 99.9.—37–38. Aff. *"Tricolporopollenites" triangulus* Groot et al., 1961; upper Subzone II-B (lower upper Albian?). Psilate tricolporoidate, two focal levels. Compare Figs. 39–42; note small size, smooth exine, and subtriangular equatorial outline. D13-555-1b, coordinates 6.1 × 98.8.—39–40. *Tricolporopollenites* sp. B, lower Zone III (lower Cenomanian?). Psilate triangular tricolporate, two focal levels. Compare Figs. 37–38, 41–42; note larger size, more elaborated colpus margins, and more triangular shape than in Figs. 37–38. D13-335-1a, coordinates 15.6 × 98.2.—41–42. *Tricolporopollenites* sp. C, Zone IV (upper lower-middle Cenomanian?). Psilate triangular tricolporate, two focal levels. Compare with Figs. 37–40; note larger size, thicker exine. 69-13-1d (clay lens in Farrington Sand member of the Raritan Formation, sand pit east of Mill Brook; New Brunswick, New Jersey, 7½-minute quadrangle), coordinates 19.6 × 96.2.—43. *Tricolporopollenites* sp. D (= Tricolporate type 3 sensu Doyle, 1969a), Zone IV (upper lower-middle Cenomanian?). Reticulate tricolporate. Compare with Figs. 33–36; note larger size, thicker exine. 68-8-1a (see Doyle, 1969a: 34), coordinates 10.4 × 102.3.—44–45. *Complexiopollis* sp., Zone IV (lower upper Cenomanian?). Early member of the triporate Normapolles complex, two focal levels. NJ 2-1b (see Doyle, 1969a: 34), coordinates 8.2 × 103.9.

monocotyledons and to the subclass Magnoliidae (sensu stricto of Takhtajan, 1969) in the dicotyledons (cf. Walker & Doyle, this symposium). *Clavatipollenites* and *Retimonocolpites* are too generalized to determine whether they were produced by monocotyledons or primitive dicotyledons, but *Liliacidites*, which extends down to the base of the Potomac sequence (Figs. 8–9), has a sculpture pattern (coarsely reticulate on most of the grain, finely reticulate at the ends and/or sulcus margins) that is now restricted to the monocotyledons (Doyle, 1973). Second, triaperturate pollen is restricted to, and apparently basic to, the six dicotyledonous subclasses other than Magnoliidae (Ranunculidae, Hamamelididae, Caryophyllidae, Dilleniidae, Rosidae, and Asteridae; cf. Walker & Doyle, this symposium). Relatively primitive reticulate tricolpate pollen is retained by many Ranunculidae, "lower" Hamamelididae (e.g., Trochodendrales, Hamamelidales) and Caryophyllidae, and a few Dilleniidae (Dilleniaceae), although it is of course unlikely that the first tricolpates would be assignable to any of these relictual and divergently specialized modern tricolpate taxa. The more advanced tricolporate condition is found in a few Ranunculidae (e.g., some Menispermaceae), Hamamelididae (e.g., Fagaceae), Caryophyllidae (e.g., Polygonaceae), and appears to be basic to Rosidae, Asteridae, and Dilleniidae exclusive of Dilleniaceae. Successive stages in the size and structure elaboration trends seen in Zones III and IV are preserved within modern tricolporate alliances: the more primitive, small, smooth type is seen in Cunoniaceae and many other Saxifragales in the Rosidae, and in Theaceae-Ternstroemioideae, Ochnaceae, Flacourtiaceae, and Elaeocarpaceae in the Dilleniidae, while most other families in the same subclasses (e.g., Rutaceae, Nyssaceae, Celastraceae, Rhamnaceae, Theaceae-Camellioideae, Tiliaceae, etc.) have larger, structurally more elaborated forms (cf. Walker & Doyle, this symposium). Finally, the advanced triporate pollen type is prevalent among many of the classic "Amentiferae" or higher Hamamelididae (Betulaceae, Myricaceae, Casuarinaceae, Rhoipteleaceae, Juglandaceae, Urticales), though forms showing the specializations of modern amentiferous families and orders do not become differentiated until near the end of the Late Cretaceous (Wolfe, 1973).

These broad conclusions on the relative advancement of groups are generally consistent with so-called "ranalean" theories of angiosperm evolution (such as form the basis of the Takhtajan and Cronquist systems), and clearly contradict theories that the "Amentiferae" are relatively primitive within the angiosperms. More direct inferences on the phylogenetic relationships of major modern groups are possible if we consider the evidence for single versus multiple origin of specific pollen characters. On the one hand, all the triaperturate types in the Potomac-Raritan sequence can be traced back into a morphologically generalized complex of tectate-reticulate tricolpates. Hence, although the existence of so many parallel trends involving size and sculpture in both monosulcate and triaperturate groups makes us wary of other parallelisms, the Potomac evidence is consistent with a single origin of the tricolpate condition and hence the hypothesis that the six non-magnoliid dicotyledonous subclasses form a monophyletic group. Because no modern families (except Nymphaeaceae sensu lato) or even orders or subclasses in the system of Takhtajan (1969) include both monosulcate and tricolpate

members, this possibility is consistent with comparative evidence. However, this question cannot be considered resolved until detailed investigations of sequences in other areas reveal actual intermediates in the origin of tricolpates. On the other hand, the fossil evidence clearly indicates that the tricolporate condition arose independently in many tricolpate lineages. Hence modern tricolporates form a highly polyphyletic assemblage, as the coexistence of tricolpates and tricolporates in many alliances would indicate (cf. Walker & Doyle, this symposium; and above).

The inferred evolutionary sequence from tricolpates through triangular tricolporates to triporates of the Normapolles type also raises doubts concerning the proposed close relationship (Cronquist, 1968; Takhtajan, 1969) of the triporate "Amentiferae," or higher Hamamelididae, to the Hamamelidales. In the later Upper Cretaceous, certain lineages of the Normapolles complex grade morphologically into pollen assignable to the Juglandales (Wolfe, 1973), and other higher Hamamelididae have also been considered as Normapolles derivatives (Góczán et al., 1967; Doyle, 1969a). The closest relatives of the higher Hamamelididae should thus be sought among groups with triangular tricolporate pollen, such as primitive Rosidae (e.g., Cunoniaceae), rather than among Hamamelidales, which have reticulate tricolpate pollen. Such a suggestion is consistent with interpretations of the foliar morphology of Juglandales (Wolfe, 1973; Hickey & Wolfe, this symposium), which indicate that they are allied to Rosidae. We thus raise the question as to whether Rosidae and Hamamelididae are as unrelated as assumed in the Takhtajan/Cronquist systems.

Many phylogenetic implications of the later Cretaceous and Tertiary pollen record, especially as related to the first appearances of pollen types assignable to particular modern families, are discussed by Muller (1970). Here we will cite only the appearance of distinctive pollen types allied to palms (and palm megafossils: cf. Read & Hickey, 1972; Doyle, 1973) late in the Upper Cretaceous (Senonian), of graminoid pollen near the Cretaceous-Tertiary boundary (cf. Jardiné & Magloire, 1965), and of pollen of many characteristically herbaceous dicotyledonous families in the middle to late Tertiary (e.g., Compositae, Acanthaceae, Labiatae).

LEAVES

Recent reinvestigations of mid-Cretaceous leaves, although less complete than the pollen studies, have contradicted early attempts at systematic identification (e.g., Fontaine, 1889; Berry, 1911) and the resulting concept of a highly differentiated Cretaceous angiosperm flora (Pacltová, 1961; Wolfe, 1972), and in fact reveal a pattern of increasing morphological diversity similar to that seen in the pollen record (Doyle & Hickey, 1972, in press; Hickey & Doyle, 1972).

In the Potomac Group, Zone I leaves (Aptian-lower Albian?) include both an apparently herbaceous monocotyledon (Doyle, 1973) and a limited diversity of simple, pinnately veined dicotyledons (Doyle & Hickey, 1972, in press; Wolfe, 1972). The irregularity in course of the secondary veins and the poor differentiation of vein orders correspond to the "first rank" venation pattern, which Hickey (1971) had concluded on the basis of comparative studies is the primitive condition in the dicotyledons (cf. Hickey & Doyle, 1972). The joint occurrence

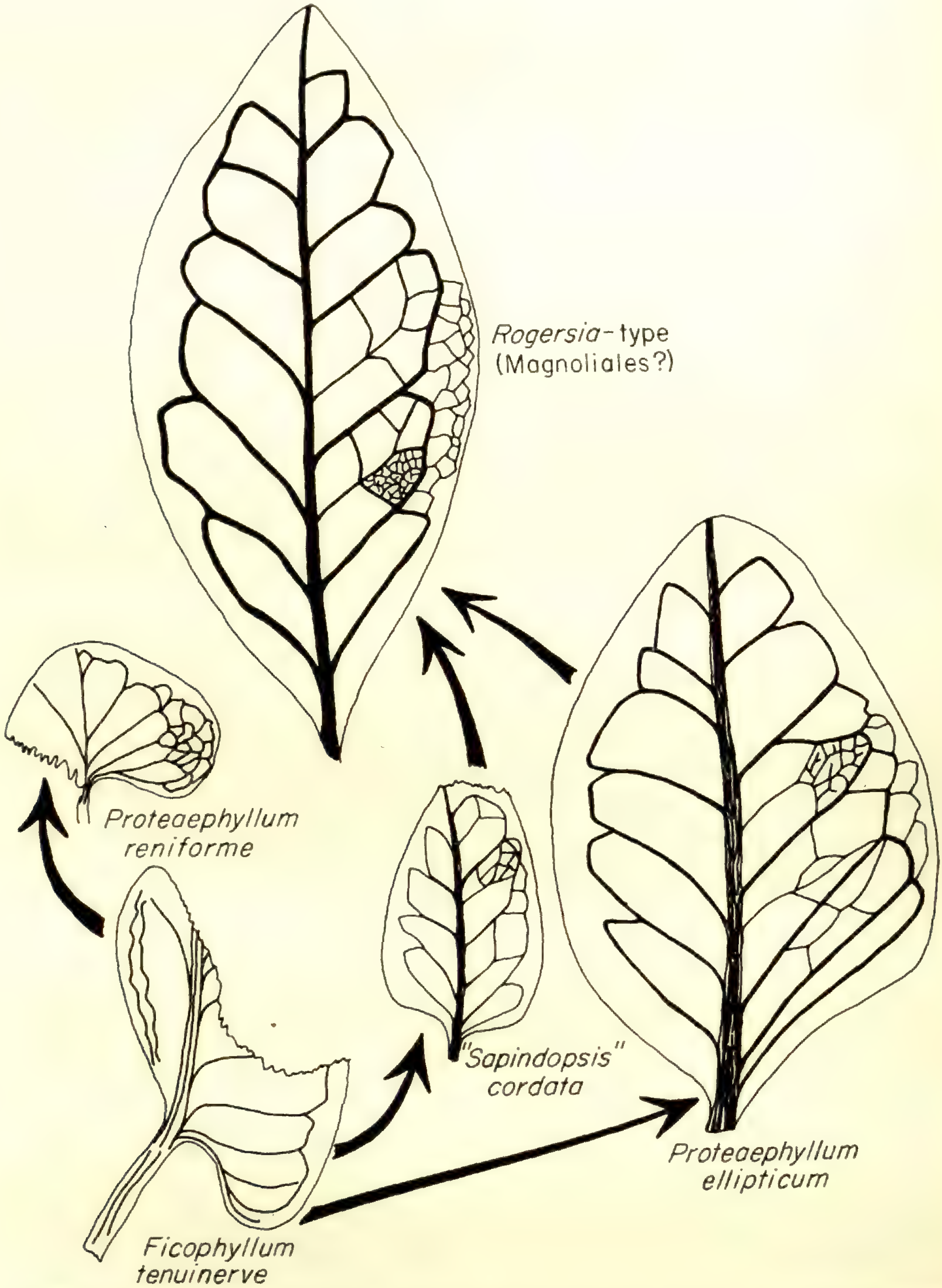


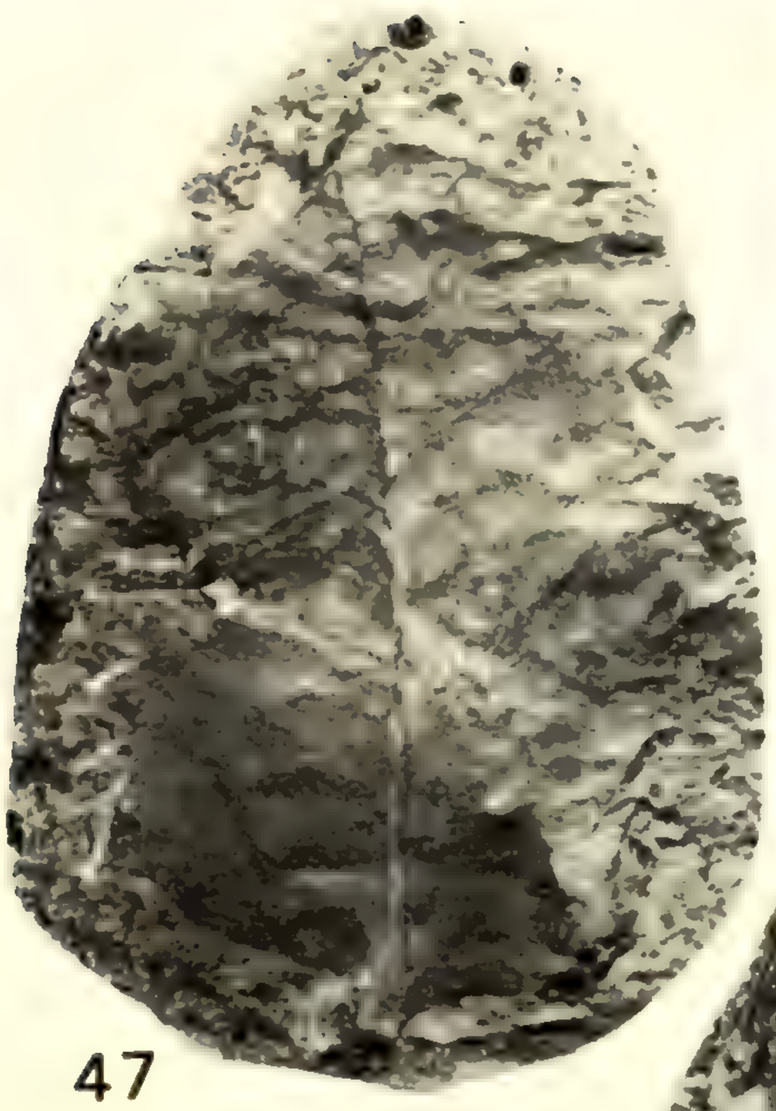
FIGURE 46. Suggested phylogeny of morphological types represented by dicotyledonous leaves from the Fredericksburg locality (lower? Albian) of the Patuxent Formation, Virginia.

of foliage of this type with tectate-columellate monosulcate pollen, moreover, is an indication that at least some of this pollen was produced by dicotyledons.

The most prolific locality for early Potomac leaves is Fontaine's locality at Fredericksburg, Virginia (upper Zone I: lower Albian?), where approximately ten species of dicotyledons are represented. Although all are coeval, they can be interpreted as a morphological series (Fig. 46); it might be expected that intermediate forms as well as the older and younger would be present in the same assemblage if we are witnessing the initial radiation of the dicotyledons. The most poorly organized type is that called *Ficophyllum tenuinerve* (Fig. 50): the midrib is composed of at least three discrete strands, and the thin, decurrent secondary veins diverge at highly variable angles to loop weakly and irregularly well within the margin. The intercostal venation is poorly developed, lacks obvious tertiary bracing and could not have given much structural support to the lamina. From such a type, which is decidedly reniform, it would be a short step to *Proteaephyllum reniforme* (Fig. 51), which has a stronger series of loops and a more pronounced intercostal venation; *P. reniforme* also shows a tendency toward a palmately veined condition (actinodromy), and it is tempting to suggest that actinodromous leaves found higher in the Potomac section represent a continuation of this trend (Doyle & Hickey, in press).

Probably the more significant trend is that represented by *Proteaephyllum ellipticum* (Fig. 49) and "*Sapindopsis*" *cordata* (Figs. 47–48; not to be confused with the type of *Sapindopsis* mentioned later). In these forms, the midrib is, except near the base, organized into one thick strand. The angles of divergence of the secondary veins are more uniform, and the secondaries are supported by thin but definite tertiary braces. A fourth order of venation is also present. Although still having a broad base, these forms are not peltate. The most highly organized forms represent at least four species, variously referred to *Ficophyllum*, *Ficus*, *Salix*, and *Rogersia* (Figs. 52–53). The *Rogersia* type clearly has a reticulation more consistent in shape and size than these other forms, and the widest part of the lamina is at or above the middle. To these four forms—all of which are entire-margined—can be added two toothed forms that have the same basic venation type. The teeth are, however, unusual in having no glands and in that the veins do not reach the outermost part of the tooth. Comparison with leaves of extant dicotyledons indicates that the more organized leaves at Fredericksburg correspond to a grade represented today only in the Magnoliidae and particularly in the Magnoliales (e.g., Winteraceae, Himantandraceae, and Canellaceae, although it is unlikely that the fossils represent any of these extant families). The grades represented by other Fredericksburg forms are even more disorganized and may indicate the existence of more primitive dicotyledons than any now extant.

Also present in the Fredericksburg dicotyledonous assemblage is the leaf called *Eucalyptophyllum* (Fig. 54). Although the venation is closed by an intramarginal vein as in many extant dicotyledonous groups (e.g., Myrtales, Ochnaceae, Dioncophyllaceae, Myrsinaceae), the intercostal venation is classed as Hickey's first rank. That is, the gross architecture is basically different from Magnoliales but the morphological grade is just as low as in many members of Magnoliales or other Fredericksburg dicotyledons. Such a leaf could well



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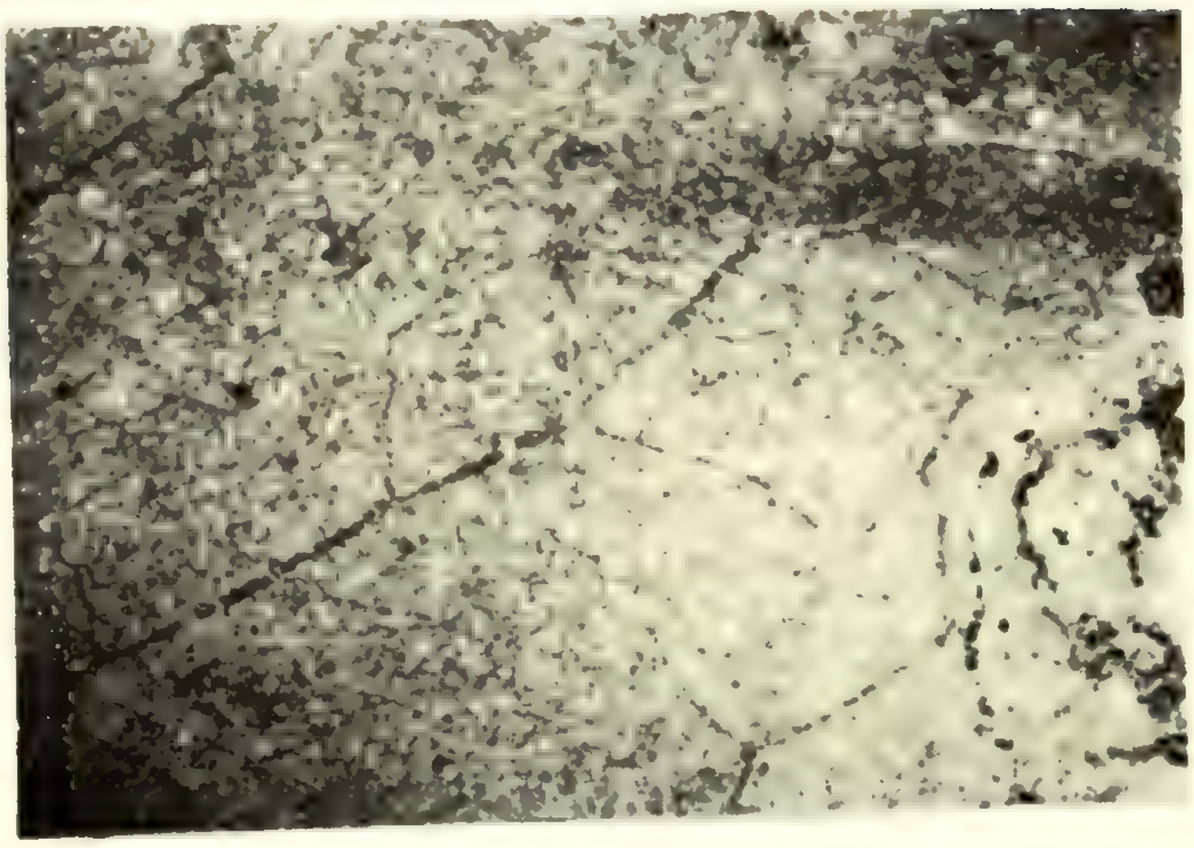

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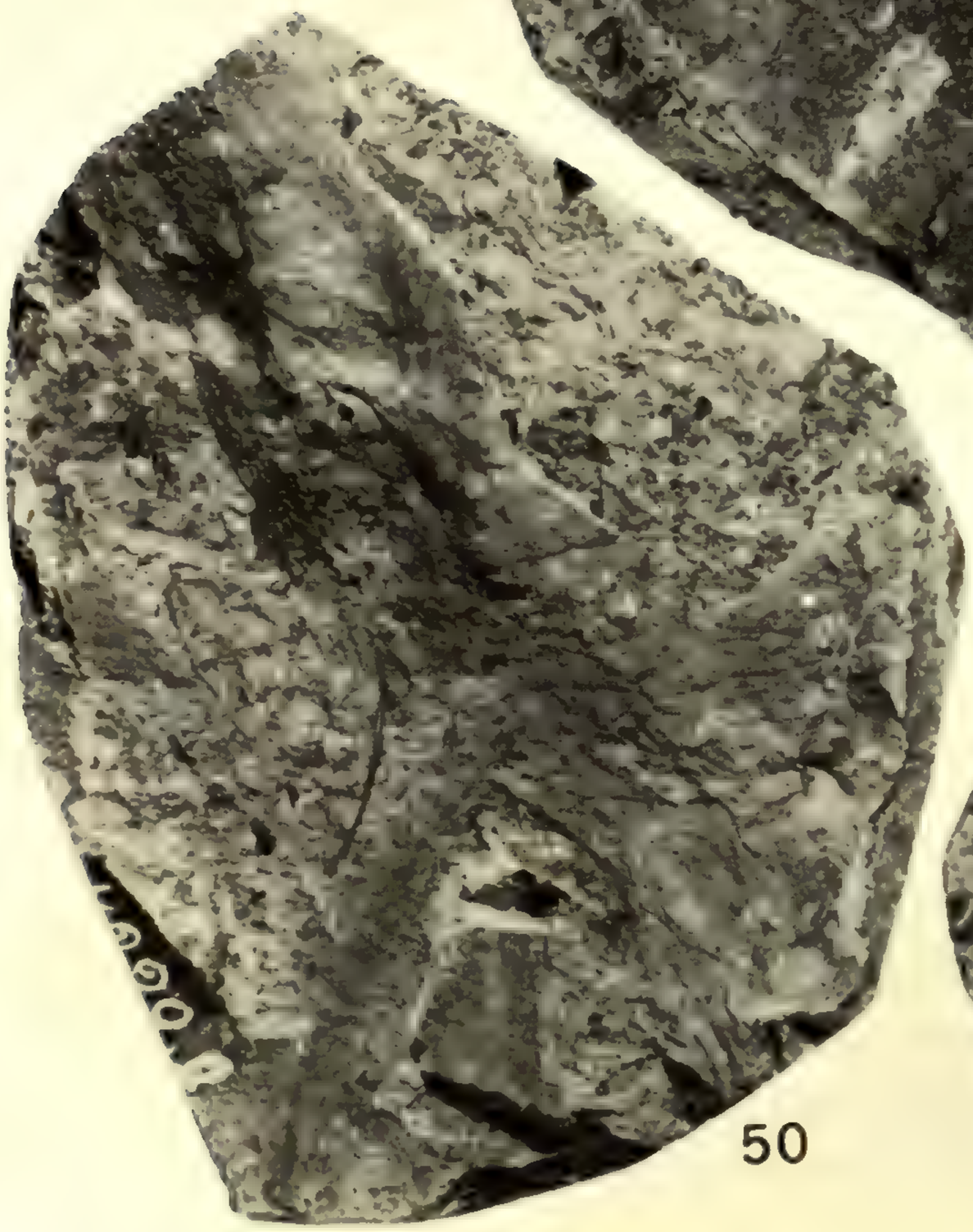

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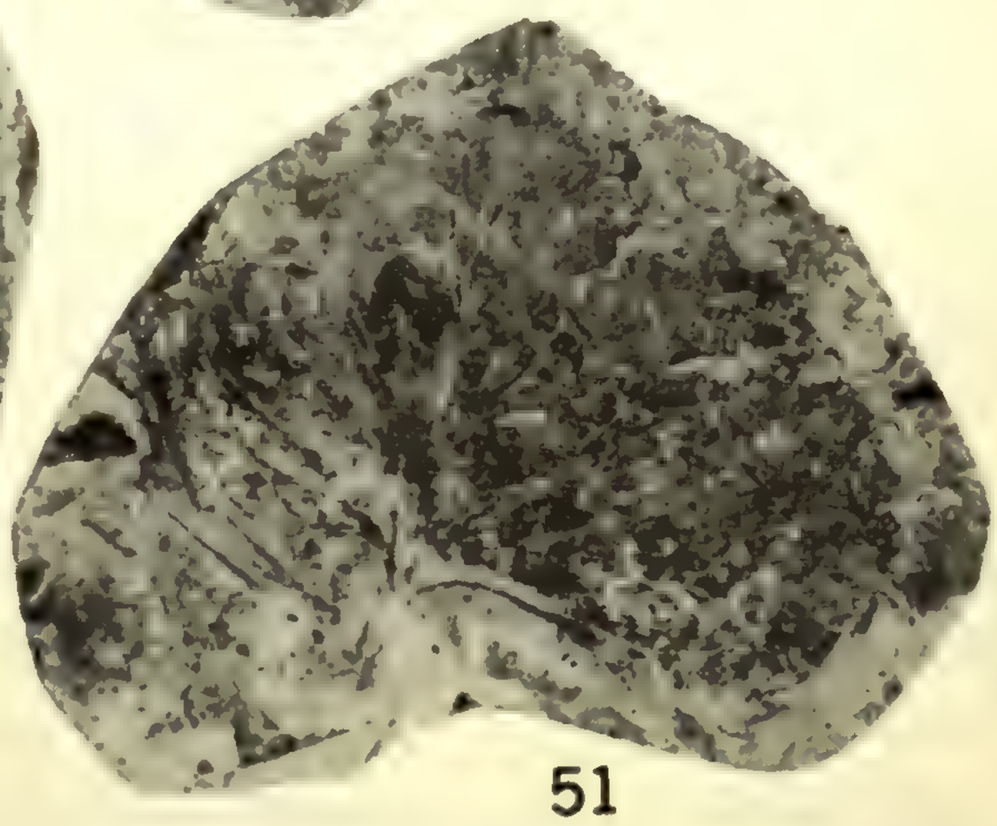

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represent an extinct line that attempted organization of the venation in a basically different fashion than in the magnolialian line (Wolfe, 1972). Such pronounced examples of morphological experimentation make dubious any attempts to assign other early angiosperms to extant families or even orders.

Higher in the Potomac sequence (Subzones II-B and II-C of Zone II: middle and upper Albian?), dicotyledonous leaves become progressively more diverse in shape and venation patterns, including peltate, ovate-cordate, and variously lobate forms (Doyle & Hickey, 1972, in press). Within this interval, several lines achieve first "second rank" (with secondary veins regular in course and spacing), then "third rank" venation (with regularly oriented, percurrent tertiary veins; Hickey & Doyle, 1972).

One of the most conspicuous lower Subzone II-B leaf types is the pinnatifid genus *Sapindopsis*. In these leaves, the venation is still disorganized as in the magnolialian grade leaves at Fredericksburg, but the lamina is deeply dissected. Indeed, the more basal segments could properly be called leaflets, but the apical segments are continuously joined. The apical segment, moreover, typically has two strong veins entering the lobes. Higher in Subzone II-B are specimens of *Sapindopsis* that are truly pinnately compound (Doyle & Hickey, in press); that the pinnatifid and compound leaves are related is indicated both by similarities in venation and Mersky's (1973, and unpublished) studies of the cuticles, which demonstrate similar epidermal patterns. Correlative beds in Kansas and Kazakhstan have yielded pinnately compound *Sapindopsis* specimens that are toothed (*Sapindopsis belviderensis* Berry, 1922; "*Anacardites*" *neuburgae* Vakhrameev, 1952); the veins entering the teeth first bifurcate, sending one branch to the sinus and the other branch along the apical side of the tooth (Doyle & Hickey, in press). In terms of extant plants, such a relationship between teeth and venation is restricted to members of Rosidae (and derivative Asteridae), in which the pinnately compound condition is also prevalent (Wolfe, 1973; Hickey & Wolfe, this symposium). These species of *Sapindopsis* in the late Albian had reached the grade of foliar morphology characteristic of Rosidae, and we suggest that this series mirrors the evolution of Rosidae from dicots at a magnoliid evolutionary grade.

WOODS

One of the major evidences cited for a pre-Cretaceous diversification of angiosperms is the putative diversity and high morphological grade of vesselled woods described by Stopes (1913, 1915) and attributed to the Lower Greensand (Aptian) of England. As in early descriptions of Lower Cretaceous leaves, some of the Lower Greensand woods have been assigned to extant families (Theaceae, Dipterocarpaceae) that are at least moderately advanced in the systems of Cronquist and Takhtajan.

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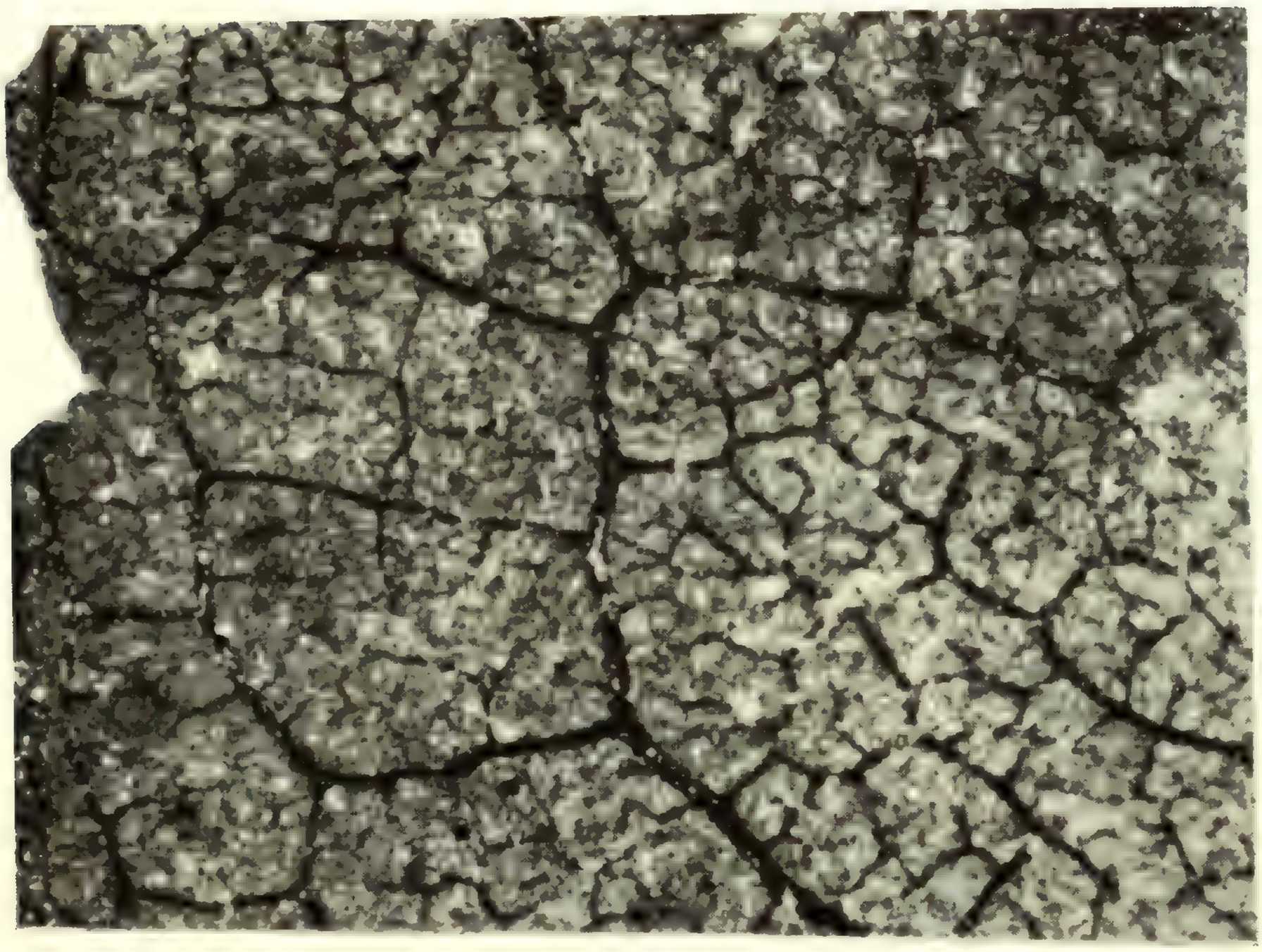
FIGURES 47–51. Dicotyledonous leaves from the Fredericksburg locality (lower? Albian) of the Patuxent Formation, Virginia.—47–48. "*Sapindopsis*" *cordata* Font., USNM 3229a.—49. *Proteaephyllum ellipticum* Font., USNM 3267.—50. *Ficophyllum tenuinerve* Font., USNM 3229a.—51. *Proteaephyllum reniforme* Font., USNM 3915.



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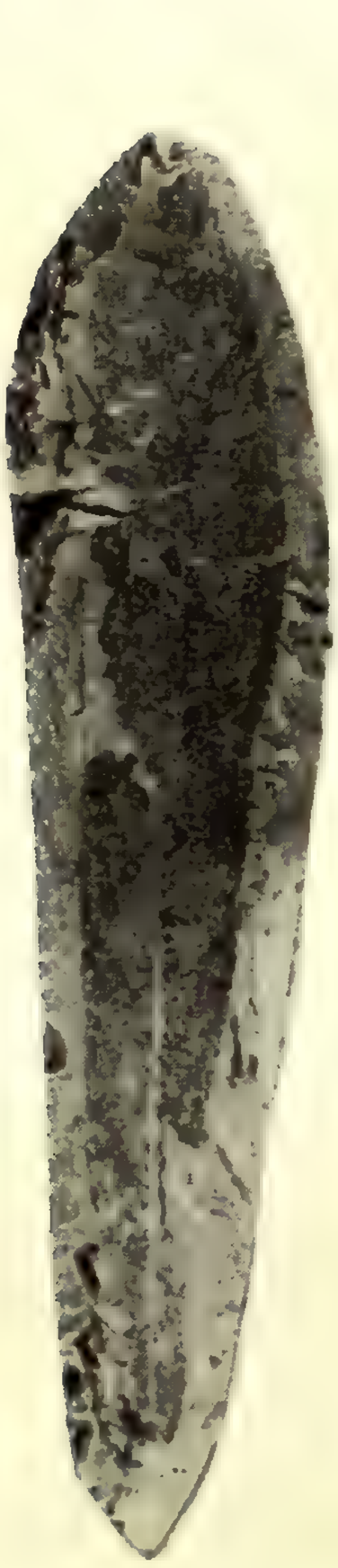

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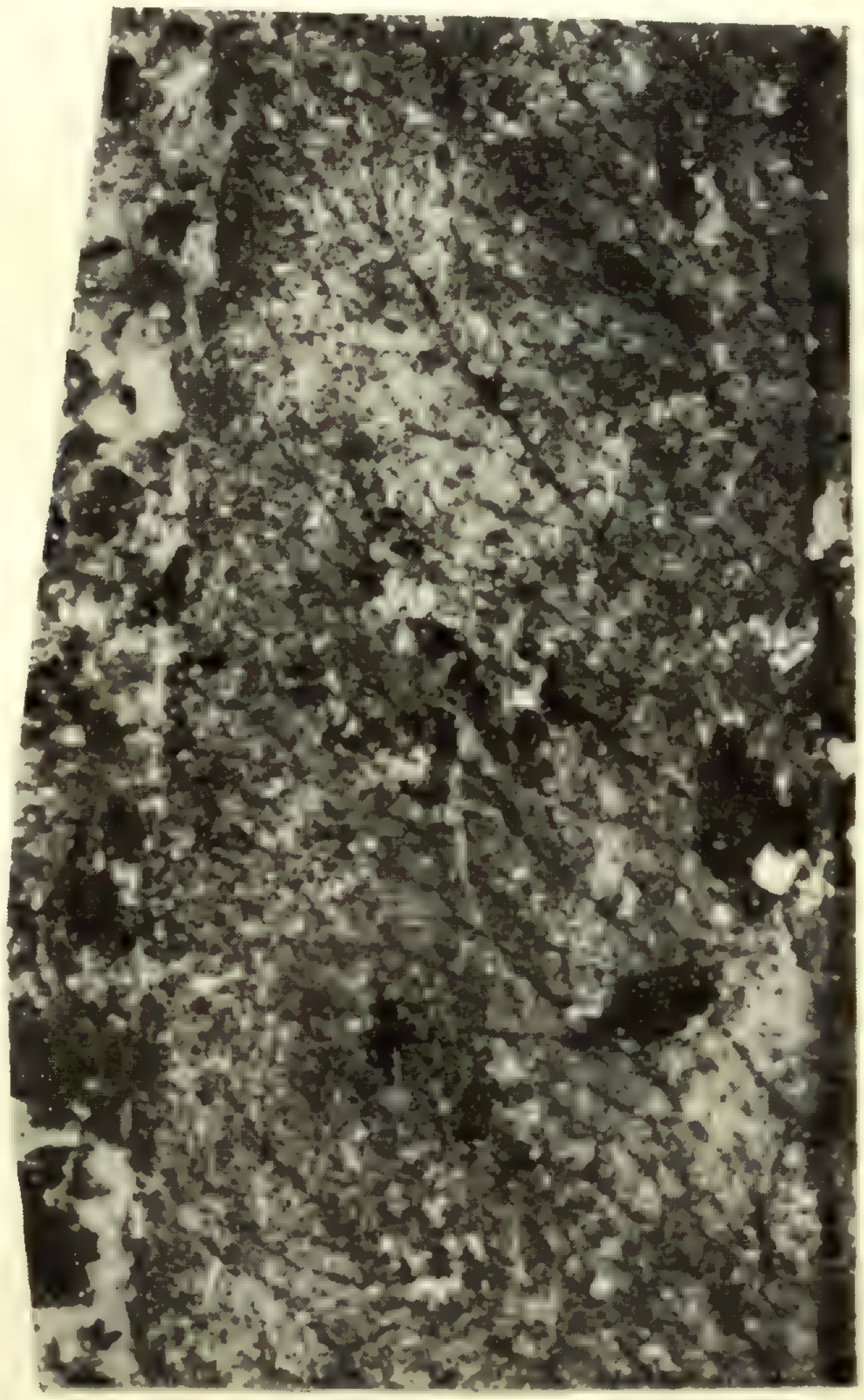

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The geologic horizons from which Stope's (1913, 1915) woods were actually derived have been validly questioned by some workers (e.g., Hughes, 1961; Harris cited in Casey, 1961). The doubts concerning the derivation are based on the fact that (1) the specimens were separately collected, deposited in local museums, and years later transferred to the British Museum, where Stopes first examined them, (2) the locality labels accompanying the specimens are vague (e.g., the specimen of *Hythia* reads: specimen presented by the Committee of the Maidstone Museum, date of collection and precise locality unknown), and (3) despite extensive geologic investigations of the Lower Greensand since 1915, no angiosperm wood has been recovered. On the other hand, Casey (1961) stated that the matrix of three of the specimens (*Hythia*, *Aptiana*, *Cantia*) matched well the lithology of the Lower Greensand (the other two specimens lack matrix), thus offering some support for the supposed age of these three specimens. One of the woods having matrix, *Cantia*, is supposedly from the Folkestone Beds at the top of the Lower Greensand and is thus of early Albian rather than Aptian age.

The two specimens—those of *Woburnia* and *Sabulia*—that lack matrix are, interestingly, the structurally most specialized (under current concepts in comparative anatomy) of the Lower Greensand woods. We suggest that these two woods are of highly questionable derivation and further consideration of them is valueless. The remaining three woods, because they may in fact have been collected from the Lower Greensand, are worthy of attention.

The wood called *Hythia* is apparently the oldest of the three (early part of the late Aptian). Interpretations of structure in this specimen are made difficult by the poor lignification of the cell walls, which led Stopes (1915) to conclude that the wood was originally "very soft." In some features (e.g., large pores or vessels), the wood is specialized, but in other features (e.g., solitary pores, scalariform perforation plates, apparently heterogeneous rays, diffuse parenchyma) it is not particularly advanced.

Even less specialized is the latest Aptian *Aptiana*. The solitary pores are only half again as large as the fibers in cross section; the rays are heterogeneous and are composed of large, square and upright cells in radial section and the multiseriate rays have long, uniseriate margins of upright cells. On both radial and tangential walls of the fibers, bordered pits occur in uniseriate or biseriate rows. The type of pitting in the vessels is not certain but the vessels may have scalariform perforation plates. The parenchyma is diffuse. This morphological grade can be found today among the putatively primitive families of all major groups of dicotyledons and could be regarded as advanced only in possessing vessels, i.e., this pattern is only one morphological grade higher than the vesselless condition.

The lower Albian *Cantia* is possibly somewhat more specialized, but the small

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FIGURES 52–54. Dicotyledonous leaves from the Fredericksburg locality (lower? Albian) of the Patuxent Formation, Virginia.—52. "*Sapindopsis*" *elliptica* Font., USNM 3261 (*Rogersia* type).—53. *Rogersia angustifolia* Font., USNM 3236a.—54. *Eucalyptophyllum oblongifolium* Font., USNM 3273.

solitary pores, square and upright ray cells, and scalariform perforation plates are unspecialized features. None of these three woods has wood patterns more specialized than patterns found in advanced members of Magnoliidae. We suggest that these three woods are consistent with our interpretations of the pollen and leaf record, that is, there is no evidence that these woods represent a morphological grade more advanced than that now found in Magnoliidae. On the other hand, we also emphasize that until such time as vesselled dicotyledonous woods have been recovered with certainty from the Lower Greensand, the evolutionary significance of Stopes's woods should be viewed with caution.

An Aptian wood of known provenance and possible angiospermous affinities is known from Japan (Nishida, 1962). This homoxylic wood has many similarities to the wood of vesselless dicotyledons such as *Tetracentron* and was assigned without qualification to the dicotyledons by Nishida. While the assignment of Nishida's wood to the dicotyledons would lend support to a Cretaceous origin and diversification of the angiosperms, we emphasize that there are some doubts as to the validity of this assignment. The fossil, which has pitting on the tangential as well as the radial walls, contrasts with extant vesselless angiosperms in which scalariform pitting occurs only on the radial walls of tracheids. The fossil also has disorganized multiseriate rays; in similar extant woods, the rays have a definite pattern of organization except typically near the departure of a branch. Indeed, rays typically become both enlarged and disorganized in such regions, and it is possible that the fossil, in which multiseriate rays are described as being rare, came from a stem that was typically uniseriate; the uniseriate condition is unusual in extant vesselless dicotyledons.

Thus, of the three putative dicotyledonous woods of Aptian age, one is vesselless and one is of an apparently very primitive vesselled type. Certainly more information is needed to establish trends and levels of advancement in the woods of the early angiosperms; only with such information can concepts of phylogeny and concepts of the relative primitiveness of anatomical features be properly evaluated.

Other reports of reliably dated and well documented Cretaceous dicotyledonous woods are, unfortunately, rare. One assemblage of 70 entities from the late Campanian or early Maestrichtian of California (Page, 1967, 1968, 1970, and unpublished) and a second assemblage of five entities from the Maestrichtian of Illinois (Lawrence Matten, unpublished) tend to substantiate that the supposedly advanced anatomical features are, in fact, geologically more recent than supposedly primitive features. Over half these wood patterns have solitary pores or solitary with a few short radial chains, and the majority also have diffuse axial parenchyma only (the remainder have some vasicentric parenchyma in addition). Similarly, scalariform perforation plates are found in the majority and the rays are heterogeneous in almost all these woods. Two of the entities are dicotyledons lacking vessels. Some of the woods do have some specialized elements, such as short vessels and aggregate rays, but the overall pattern of these woods is not advanced. None of the woods possess supposedly advanced features such as storied elements, included phloem, aliform or confluent parenchyma, or elaborate pore distribution. Although many of the specimens may represent young stems

in which the mature patterns might have been more specialized, we think that it is highly significant that as late as the Maestrichtian, wood patterns had apparently reached only a moderate level of specialization.

Patterns at the same grade of specialization as those encountered in about half of Matten's and Page's woods occur today in less than 30% of the families of woody dicotyledons. That is not to say that all members of these families have this same grade, because many members may have much more specialized patterns. Aside from members of Magnoliidae, such less specialized patterns occur in the supposedly more primitive members of Dilleniidae (e.g., Dilleniaceae, Theaceae, Flacourtiaceae, Symplocaceae, Saurauiaceae, Daphniphyllaceae, Dichapetalaceae), less frequently in the Rosidae (e.g., Cunoniaceae, Hydrangeaceae, Aquifoliaceae, Cornaceae), Hamamelididae (e.g., Cercidiphyllaceae, Eupteleaceae, Hamamelidaceae, Myricaceae), and only in one family of Asteridae (Caprifoliaceae). Indeed, some of the California woods are considered to be allied to Magnoliales, Laurales, Trochodendrales, Ranunculales, Hamamelidales, and Saxifragales (Page, 1967, 1968, 1970).

Post-Cretaceous Diversification

That major angiosperm diversification continued following the Cretaceous is indicated by a taxonomic analysis of the London Clay flora, an early Eocene assemblage based on fructifications. Comparing this assemblage of about 350 dicotyledonous species with the vegetationally comparable flora of lowland Taiwan (471 species), it can be seen that specific diversity within Magnoliidae has drastically declined since the Eocene. In the London Clay flora, fully 25% of the species belong to Magnoliidae, whereas only 8% of the Taiwan species fall into this subclass. More significantly, whereas the lowland flora of Taiwan has representatives of 14 families of woody Asteridae, the London Clay contains but four, and notably lacking are Asclepiadaceae, Rubiaceae, and Verbenaceae. At the generic level, the London Clay flora contains but six members of Asteridae, in contrast to the 54 represented in lowland Taiwan. Such comparisons are consistent with the well-known first appearance of presumed advanced Asteridae, such as Compositae, near the Oligocene-Miocene boundary. Clearly, paleobotanical work to assist in the unraveling of the phylogeny of the angiosperms at higher taxonomic levels will involve work not just in the Cretaceous but also in the Tertiary (cf. Muller, 1970).

Conclusions

This report has, we hope, shown both the potential value of paleobotany to interpretations of phylogenetic relationships among extant angiosperms and the need for much additional work on the paleobotany of the angiosperms. Specifically, paleobotany strongly supports the primitiveness of Magnoliidae relative to the other subclasses of the dicotyledons. The evidence also indicates that the split between the monocots and dicots occurred early and prior to either class having attained even a moderate level of advancement. The earliest tricolpate pollen is small and finely sculptured, the same type that occurs in putatively primitive members of Hamamelididae and in the Ranunculidae; the geologically

younger and derived tricolporate grade is basic to subclasses Rosidae, Asteridae, and Dilleniidae (except Dilleniaceae). The pollen type possessed by the higher Hamamelididae or Amentiferae, p.p., and the Rosidae is younger geologically than the type possessed by putative ancestors. Fossil foliage provides a gradational series from a type now characteristic of Magnoliales to a type basic to Rosidae. The evidence may indicate, however, that Hamamelididae and Rosidae are more closely related than the Takhtajan-Cronquist system suggests. Our interpretations of the Early Cretaceous pollen and leaf records indicate that the evolutionary rates were comparable, i.e., both leaf and pollen records display an increasingly higher level of morphological complexity in the same sequence. We also suggest that as studies in critical areas, both geographically and geologically, are carried out, paleobotany will make an increasingly significant contribution to an understanding of the phylogeny and classification of the angiosperms.

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DEDUCTIONS ABOUT TRANSSPECIFIC EVOLUTION THROUGH EXTRAPOLATION FROM PROCESSES AT THE POPULATION AND SPECIES LEVEL[1]

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Abstract

Information about the basis of transspecific evolution can be obtained only by extrapolation from processes known to take place at subspecific levels. Given sufficient information, such extrapolation is justified by the fact that no processes can be detected at the transspecific level which are different from those that operate at subspecific levels. Nevertheless, certain shifts must be recognized: particularly, greater emphasis on alternative evolutionary strategies, and the greater importance of reproductive as compared to vegetative characters. In addition, the long time span required for transspecific evolution means that many reversals of evolutionary direction can be expected, and common ancestors of modern families and orders are likely to be extinct. Evolutionary conservatism depends upon the complexity of the developmental pattern of a character, and the uniformity versus diversity of the selective pressures to which it might be subjected. Reversibility of evolutionary trends depends upon the number of separate genetic changes needed to produce the change in the original direction. The effect of these deductions on the most widely accepted phylogenetic systems is slight. Principally, weighting of individual characters is regarded as unjustified, linear relationships between modern families are highly unlikely, and cross sectional phylogenetic charts are preferable to the conventional "trees."

At the level of populations and species, the study of evolutionary processes is an exact science. The knowledge which geneticists have now acquired about the extent and organization of hereditary variability in populations, as well as quantitative determinations of the rates at which natural selection can bring about changes, make possible definite predictions which can be tested by means of carefully controlled, quantitative experiments.

This precision, however, is possible only if genetic differences can be estimated by hybridizing different genotypes, and obtaining genetic ratios in the later generation progeny. Consequently, when we are dealing with entities so distantly related to each other that hybridization is either impossible or gives rise only to sterile offspring, the precision of analysis becomes progressively lower. Direct analysis of genetic relationships between genera, families, and other higher taxa is impossible or of only limited application. We can understand evolution at transspecific levels only by extrapolating from results obtained at subspecific levels. Is such extrapolation justified?

The Justification of Extrapolation

Successful extrapolation requires making valid and complete analogies, which are possible only if the proportion of unknown factors is relatively small. For instance, if I knew nothing about the growth of a human child, and should discover that my first born son, originally weighing eight pounds at birth, had

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gained 16 pounds during his first year, I might hypothesize that he would gain twice his starting weight every year, and would weigh 216 pounds at the age of three. Alternatively, I might postulate that he would gain 16 pounds per year throughout childhood, and so would weigh 184 pounds at the age of 11. I would still be wrong, but the absurdity of this conclusion would be less obvious. On the other hand, if I had complete statistics on my own weight and that of my wife during our first ten years, plus similar information on children of relatives who had received nourishment similar to that which I would give to my own son, I could reach a sufficiently accurate estimation of what his weight would be at various ages. In my opinion, the best way of looking at the present symposium is as a major effort to bring together all of the existing knowledge about angiosperm evolution above the species level, and to assess its value in making extrapolations.

We might feel satisfied if our final result is a better description of the course which angiosperm evolution took, as judged from affinities between modern taxa. Nevertheless, we shall fully understand our problem only if our extrapolation can be extended to the formulation of hypotheses about the processes which guided the course of evolution into the numerous and diverse pathways which it has followed. Before we can make this kind of extrapolation, we must first ask ourselves: "are there any processes operating at levels of higher taxa that are unknown at the levels of populations and species." If there are, extrapolations about processes are certainly impossible, and any hypotheses that we might make about phylogeny would be highly suspect.

Fortunately, however, modern molecular biology has effectively disposed of this problem. In addition to mutation, gene recombination, chromosomal repatterning, and natural selection, which are now reasonably well understood at the level of populations and species, two other processes have been postulated by botanists concerned with phylogeny, neither of which can be recognized at the subspecific level. These are (1) "macromutations," which could at one step give rise to a population belonging to a new genus, family, or order; and (2) "orthogenesis," by means of which evolutionary direction is believed to be determined not by interactions between populations and their environment, but by directed mutations occurring within the genotype, unaffected by the environment.

The implausibility of both of these hypotheses has long been recognized by evolutionary geneticists (Fisher, 1930; Dobzhansky, 1941), as well as by paleontologists who are familiar with the genetic facts (Simpson, 1953). Their virtual impossibility is dictated by the complex relationships now known to exist between genes and characters (Watson, 1970; Monod, 1971). A single gene can provide information for only one polypeptide chain. Its primary product may be a monomer enzyme, capable of catalyzing a single step in a complex biosynthetic pathway. More often in higher organisms, the polypeptide chain is part of a multimer enzyme, of a complex supra-molecular architecture of structural protein or a unit in the system of regulators that we must postulate in order to understand gene action in multicellular organisms (Britten & Davidson, 1969, 1971). Single gene mutations, therefore, can never do more than alter a single, small part of a complex, highly coordinated developmental system. If the alteration is profound, the phenotype may deviate greatly from normal, but since the harmony of

development has been violently disturbed, this mutant phenotype will always be an inadaptive monster. Major changes, such as those responsible for new genera, always take place by the accumulation of scores or hundreds of genetic differences, most of which, individually, have only small effects on the phenotype.

Orthogenetic trends, determined by mutation alone, would require that large numbers of diverse genetic changes be somehow coordinated to produce a phenotypic effect entirely different from that which one or a few of them could produce by themselves. At the gene level, the kind of mutation needed to alter one kind of structural or control protein in a direction that would favor, for instance, the "fusion" of petals would be entirely different from the kind of mutation which in another protein would contribute toward the same result. Coordination of these diverse changes is conceivable only via the action of natural selection.

This does not mean, however, that trends of evolution are governed solely by random mutations exposed independently and separately to the selective action of the external environment. Geneticists now recognize that the adaptive value of a mutation may depend as much or more upon the other genes with which it is associated in an individual genotype as upon its own interaction with the environment. The pre-existing genotype has a powerful screening effect on new mutations, which becomes ever more stringent as adult structures and their developmental pathways become more complex. If a particular evolutionary line has already evolved a radially symmetrical corolla having a short tube, mutations promoting a longer tube will be favored, while those promoting the shift to bilateral symmetry are less likely to become established. If, on the other hand, evolution toward a choripetalous, zygomorphic corolla has begun, mutations toward sympetaly are likely to be rejected and those leading toward zygomorphy tend to be favored. The consequences of this difference are explored below.

A second question which must be satisfactorily answered before we can justify extrapolation from the subspecific to the transspecific level is: are there any morphological characteristics that play major roles in the origin of genera and families, but which never appear as differences between species of the same genus? After carefully reviewing this subject, I have become convinced that there are no such characters. Even differences which are regarded as "most fundamental," such as that between hypogyny, perigyny, and epigyny, exist at the level of species differentiation in genera such as *Saxifraga*. The "fundamental" difference between monocotyledonous, dicotyledonous, and tri- or tetracotyledonous embryos and seedlings separate different species or species groups in genera such as *Pittosporum*, *Ranunculus*, and others (Stebbins, 1974).

Shifts of Emphasis Between Subspecific and Transspecific Levels

Nevertheless, the action of the evolutionary processes and the characters that they alter are different at transspecific levels from those prevalent at subspecific levels. The difference, however, is one of emphasis rather than kind. With respect to characters, a well known fact is that reproductive structures are increasingly valuable at higher levels, as compared to vegetative characters. This trend, however, is no more than a moderately high correlation, and many exceptions

exist. Vegetative characters such as cotyledon number, seedling development, wood structure, and presence versus absence of stipules are, as a rule, more important at higher than at lower levels of the taxonomic hierarchy. Among reproductive characters, those of the gynoecium are more often significant at the level of genera and families than those of the androecium and floral envelopes. The reasons for this difference are discussed later.

With respect to evolutionary processes, one phenomenon which becomes increasingly significant at higher taxonomic levels is that of alternative evolutionary strategies. For instance, the adaptive shift in flowers from insect to bird pollination must involve the appearance of a long, narrow tube which fits the bird's beak, and contains nectar at the bottom. This structure can be evolved by means of lengthening and straightening the spur on a sepal (*Delphinium*) or a petal (*Aquilegia*); by evolving a long, narrow corolla tube (*Kniphofia*, *Pentstemon centranthifolius*), or a hypanthium (*Zauschneria*, *Fuchsia*); or by evolving a corolla in which the lower parts of separate petals are much elongated and overlap each other (*Erythrina*). Response to selection for higher seed production in an evolutionary line that is occupying a progressively more favorable climatic zone can be accomplished by increasing the number of ovules per carpel, carpels per flower, flowers per inflorescence, or inflorescences per plant. Increased efficiency of seed dispersal by either wind or animals can be evolved via modifications of seeds, segments of fruits, entire fruits, fruits plus calyces, or entire inflorescences (Stebbins, 1970b, 1971, 1974). Phylogenetic trends are often determined not by the particular kind of selective pressure which is operating, but by the way in which the population or evolutionary line responds to a generalized kind of selective pressure.

Given the possibility of alternative evolutionary strategies, what determines the particular strategy which a given evolutionary line will adopt? This is determined chiefly on the basis of evolutionary canalization, a principle which states that evolutionary lines tend to follow certain pathways, the nature of which is governed by two principles: conservation of organization and adaptive modification along the lines of least resistance. These principles can be stated as follows.

Conservation of organization means that if a structure has evolved which requires for its development a complex, highly coordinated sequence of gene actions, it tends to be preserved and modified as evolutionary lines become adapted to new conditions. Even if an entirely new structure would produce a better adaptation, the complex "genetic revolution" that is required to produce it is very unlikely to take place, particularly if one part of this "revolution" involves an inadaptive intermediate stage.

Adaptive modification along the lines of least resistance means that evolutionary lines usually become adapted to new conditions by whatever changes involve the smallest number of gene substitutions. In angiosperms, these most often are quantitative alterations of the amount or the duration of activity of a particular kind of undifferentiated meristem.

The operation of these principles to determine which evolutionary strategy will be adopted in the shift to bird pollination is as follows. In *Delphinium* and *Aquilegia*, which have, respectively, spurred sepals and petals in those ancestral

species that are adapted to bee pollination, modification of these spurs is the path of least resistance. In *Pentstemon*, on the other hand, the ancestral bee pollinated species already possessed a corolla tube, the modification of which for bird pollination required relatively little adjustment of the gene-controlled developmental pattern. The Onagraceae, on the other hand, have separate petals and so lack a corolla tube, but usually have a more or less well developed hypanthium, the modification of which into a floral tube adapted to the bird's beak was the path of least resistance in the evolutionary lines leading to *Zauschneria* and *Fuchsia*. The role of evolutionary canalization in determining evolutionary strategies with respect to mechanisms for seed production and dispersal has been discussed elsewhere (Stebbins, 1967, 1970b, 1971, 1974).

These examples all illustrate a cardinal principle which operates generally at the transspecific level, but which is much less likely to be evident at the level of populations and closely related species. Given an initial diversity with respect to certain adaptive structures, response to the same kind of selective pressure is just as likely to promote their divergence via the adaption of different kinds of responses to this pressure, as to promote parallelism or convergence. In other words, whether two independent evolutionary lines will diverge, evolve parallel to each other, or converge depends both upon the similarity or difference between the kinds of selective pressures to which they are subjected, and the nature of preexisting structures which might be modified in response to these pressures.

Another factor that is of primary importance in evolution at transspecific levels is the long time span that is necessarily involved. Species can often be differentiated in as short an interval as two to a hundred generations (Grant, 1971). On the other hand, no valid genus of angiosperms known to me can be clearly shown to be less than five million years old (Pliocene), and most of them are much older. The effect of this time span is twofold. In the first place, the evolutionary history of most plant genera covers time spans during which both the earth's climate as a whole and that of local regions has oscillated from favorable to unfavorable conditions, and back again. This means that many opportunities have been available for evolutionary lines to reverse their direction of adaptational change. Such reversals have been commonplace. An example in the subtribe Microseridinae of the Cichorieae, Compositae, is discussed elsewhere (Stebbins, 1972a). I believe that whenever two groups of angiosperms exist sympatrically, and differ with respect to the advancement, specialization, or efficiency of their reproductive structure, careful analysis will show that the more advanced group has not evolved from the less advanced group in situ, but by an indirect route, involving first adaptation to different, usually more severe conditions, followed by later readaptation to the conditions that make possible the sympatry.

Another effect of long time spans is extinction. Comparisons between families having well defined genera and those in which generic lines are blurred show clearly that the distinctness of genera depends largely upon extinction of species intermediate between them and other genera (Stebbins, 1956). This extinction is most likely to effect the immediate ancestors or the earliest representatives of any highly successful group, since these forms are the most likely to come into direct competition with members of the successful group. This fact is largely

responsible for a phenomenon of primary importance in constructing phylogenetic trees. No modern, successful group, including the angiosperms themselves and the two major subdivisions of the class, Dicotyledons and Monocotyledons, can be regarded as a descendant of any other living group. Even the use of the suffix "-like" to indicate that a hypothetical ancestor was so much like some living group that, had botanists been present when it lived they would have been able to classify it in that group, is inadmissable. This contention is supported by fossil evidence whenever it is available. The seed plants which have the best fossil record are the conifers. In them, Florin (1951) has shown clearly that the common ancestors of the principal modern families, Pinaceae, Taxodiaceae, Cupressaceae, Taxaceae, and Podocarpaceae, are so different from any modern group that they could not possibly be reconstructed except on the basis of fossils. The same is true of animals generally, particularly vertebrates (Romer, 1966). There is no reason to believe that the situation in angiosperms is any different. Bailey & Nast (1945) already emphasized the profound differences that exist between all of the presumably primitive groups that are placed in the woody Ranales or Magnoliidae of Cronquist. Moreover, every one of these groups is highly specialized in at least one or two characteristics. Consequently, in the absence of significant fossils, so many unknown factors exist that the method of extrapolation is inadequate as a means of deducing what ancestral forms were like on the basis of the morphology of any living angiosperms. Such extrapolation can be very misleading.

Interpretations of Phylogenetic Trends on the Basis of Extrapolation

Even though, as has just been mentioned, the method of extrapolation is inadequate to determine actual phylogenetic relationships, except at the level of recently evolved genera within a family, it can provide valuable evidence about the general nature of phylogenetic trends, and the conditions that would be favorable to a particular kind of morphological change. In the remainder of this article, extrapolation will be used to suggest interpretations of this nature.

THE TAXONOMIC SIGNIFICANCE AND DEVELOPMENTAL-GENETIC BASIS OF EVOLUTIONARY CONSERVATISM

Characters that are valuable at the level of genera and families must have a moderate but not extreme degree of conservatism. Characters having extreme genetic plasticity, such as the size, shape, and texture of leaves, are rarely of value at these levels. On the other hand, the more conservative characters, such as roots, phyllotactic arrangements of leaves, numbers of floral whorls, ovule structure, and the nature of the embryo sac, are useful only in a relatively small proportion of groups within which they show significant variation. Characters having intermediate degrees of conservatism can either be very valuable or valueless, depending upon the group. For instance, characters of the corolla and androecium are of relatively little value in separating genera of Rosaceae, are valuable in Leguminosae chiefly at the level of subfamilies or tribes, and in Primulaceae, Scrophulariaceae, Labiatae, and other sympetalous families are among the most important characters for defining genera. On the other

hand, characters of the gynoecium are relatively important in Rosaceae and Leguminosae, but much less important in Primulaceae, Scrophulariaceae, and Labiatae. Is the degree of conservatism of a particular character within a group a purely chance affair, or it is related to factors that might be analyzed as a means of determining its adaptive basis, if any?

I would like to suggest that the degree of conservatism of a character is related to two factors: the complexity of its developmental pattern and the diversity of selective pressures to which it might be subjected. Leaves, for instance, have a relatively simple developmental pattern. If they are subjected to similar selective pressures during a long period of evolution, as is true of the leaves of most Lauraceae and Orchidaceae that inhabit tropical forests, they are too conservative to be of any taxonomic value. On the other hand, if they are subjected to highly diverse selective pressures, as in the herbaceous Rosaceae of temperate regions, they are so variable that they can serve only to distinguish closely related species and subspecies. In the Umbelliferae, the perianth has a simple developmental pattern, and is of little taxonomic value; in most sympetalous groups, particularly those that are zygomorphic, the developmental pattern of the corolla is highly complex, and it usually is sufficiently variable that its variations are of great taxonomic value. In groups having relatively small and simple corollas, which are pollinated by a variety of relatively unspecialized insects, differences in the corolla are most valuable at the level of genera. In groups having larger corollas, and pollinated by more specialized insects, or by special methods such as pseudocopulation, differences between corollas are most valuable at the level of different species within a genus.

In general, characters of the gynoecium are more likely to be significant at the level of families than are those of the androecium. I believe that this tendency toward greater conservatism of gynoecial characters is based upon two facts. In the first place gynoecia are compound structures, the parts of which (ovary wall, style, stigma, and ovules) differ greatly from each other in adaptive function. Their developmental pattern is, therefore, usually more complex than that of the corolla. Secondly, the selective pressures to which they are subjected depend more upon integration of diverse functions than upon adaptation of individual functions to specific alterations of the environment. The receptive surface of the stigma, for instance, must be adjusted to the external structure of the pollen grains, while the length of the style must be in harmony with the amount of food reserves which pollen grains possess. With respect to ovules and seeds, adaptation depends upon a number of factors that in some ways conflict with each other (Stebbins, 1971): seed size, nature of dispersal mechanisms, length of seed development period, and vigor of seedlings. The adaptive balance that any species has acquired can be altered only by coordinated changes with respect to several of these characters.

REVERSIBILITY VERSUS IRREVERSIBILITY OF EVOLUTIONARY TRENDS

As has been clearly stated by Simpson (1953: 310–311), Dollo's law of irreversibility cannot be applied to single characteristics that have a simple genetic basis. It is valid only if a particular kind of evolutionary change involves

coordinated alteration of many different characteristics, or of a single characteristic which has a highly complex developmental pattern. If one or both of the latter situations exist, the result of evolutionary canalization will be the tendency of a structure to evolve in a new direction in response to a reversal of selective pressure, rather than a return to the original state. Abundant examples of secondary reversal from wind to insect pollination exist throughout the angiosperms, but the revertants are always completely different in structural characteristics from primitively insect pollinated species (Stebbins, 1970a). A good example is the genus *Ficus* and others of the Moraceae. Secondarily derived shrubs, such as various Chenopodiaceae, Nyctaginaceae, and the genus *Artemisia* of the Compositae, are completely different in stem anatomy from primitively woody species (Stebbins, 1972b). In the Cichorieae, the genus *Tragopogon*, a mesophyte which has probably been derived secondarily from more xeric ancestors, has leaves entirely different from those possessed by primitively mesic Cichorieae (Stebbins, 1952).

With respect to single characters such as numbers of similar parts, these are determined largely by the amount of undifferentiated meristem available at the time when a particular kind of organ is being differentiated, or the length of time over which a shoot apex will possess a meristem having a particular kind of developmental potential (Stebbins, 1967). Since these developmental events are simple and quantitative, they are subject to genetically determined alterations in either direction, and hence to reversal. With respect to the number of serially produced parts, such as leaflets of a compound leaf, flowers of an inflorescence, sepals, petals, stamens and carpels or ovary locules in a flower, or ovules per locule, taxonomists in the past have tended to read the series in only one direction, usually from many to fewer parts. After considering carefully many such series, I am convinced that in the vast majority of them the true directions have been those that one would expect on the basis of adaptive radiation; from some point in the middle of the series toward an increase in some derivative lines, and a decrease in others.

Other single character differences, such as "fusion" of sepals or petals, as well as the trend from hypogyny to perigyny and epigyny, are based upon differences with respect to a complex developmental pattern, involving the initiation of an intercalary meristem at a precisely regulated stage of development, and its cessation at an equally precise stage. From the point of view of developmental genetics, such differences are comparable to differences with respect to many separate morphological characteristics, since alterations of several separately acting genes are involved. Reversal of such trends can be expected only rarely or not at all.

BEARING OF THESE DEDUCTIONS ON THE NATURE OF PHYLOGENETIC SYSTEMS

If taxonomists take into account the principles and deductions which I have discussed, they will not need to alter very much the phylogenetic schemes that have been proposed more recently for the Angiosperms, particularly those of Takhtajan (1966, 1969) and Cronquist (1968). The concept of alternative evolutionary strategies predicts that certain kinds of major alterations of the flower,

such as the origin of sympetaly, epigyny, and the herbaceous growth habit will be repeated independently in many different groups, so that similarity with respect to such characters is not by itself evidence of relationship. The principal differences between the Cronquist-Takhtajan system and the older ones that resemble it are of this nature. The extrapolation of the concept of adaptive radiation to transspecific levels predicts that modern families can rarely be arranged in a linear series from most primitive to most advanced: the evolutionary "tree" is actually a much branched shrub. This form is characteristic of the Cronquist-Takhtajan system.

Two of the conclusions reached here do affect the nature of the Cronquist-Takhtajan system to some extent. First, because of the complex relationships between changes at the gene level and the alteration of morphological characters, as well as the importance of preexisting characters in determining the direction of evolution, the weighting of individual characters which regards some as of critical importance in determining the phylogenetic position of a group, and others as much less important, is unwarranted, at least in our present state of knowledge (Stebbins, 1974). Second, the high probability that the common ancestor of any two modern families or orders is extinct, and cannot be reconstructed by extrapolation from modern forms means that all phylogenetic trees are suspect. Much more realistic are cross sectional diagrams, such as those of Rodriguez (1956) and others which show relationships between modern groups without specifying the precise evolutionary pathways by which they arose. Phylogenetic primitiveness or advancement can be expressed by placing the orders at varying distances from a central point, which expresses in a very general way the characters of a hypothetical common ancestor, without attempting to describe or name it. This is, admittedly, not very satisfying for those taxonomists who wish to believe that we understand the directions of angiosperm evolution. Nevertheless, it is realistic: the unpleasant but inescapable fact is that, lacking an adequate fossil record, the evolutionary relationships between modern subclasses and orders of Angiosperms may never be fully understood. Our systems must reflect our ignorance as well as our knowledge.

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FLORA OF PANAMA[1]

BY ROBERT E. WOODSON, JR. AND ROBERT W. SCHERY
AND COLLABORATORS

Part IX

FAMILY 184. COMPOSITAE[2]

Mostly *herbs*, sometimes *shrubs*, *trees* or *vines*, variously pubescent or glandular, sometimes glabrous; stems terete, sometimes winged or flattened into cladodes, sometimes fistulose. *Leaves* alternate, verticillate, or opposite, sometimes basal, rarely reduced to scales, spines, or wanting, simple or 2- to many-foliolate, entire or variously toothed, lobed or dissected; petioles present or wanting; the leaf bases sometimes decurrent or clasping; stipules wanting but pseudostipules sometimes present. *Inflorescences* cymose, racemose, paniculate, umbellate, or of solitary heads, the heads sometimes in indefinite aggregates; peduncles mostly present but sometimes wanting and the heads then often in glomerules; bracts often present; pedicels mostly present, sometimes bracteolate. *Heads* of 1–many florets (flowers) situated on a receptacle (torus), basally enclosed in an involucre and sometimes interspersed with paleas (chaff), the floret arrangement radiate, disciform, discoid, or ligulate, the outer or inner florets sometimes sterile; involucral bracts few–many in 1–several similar, differentiated, or evenly graded series, free or connate, valvate or overlapping, those of the innermost series sometimes enfolding the florets; receptacle depressed, flat, globose, conical, or obsolete; paleas characteristic of some groups, flat or enfolding the florets, sometimes reduced to hairs or short scales, or wanting; outer florets, when differing

[1] Assisted by National Science Foundation Grant BMS 72-02441 A03 (Thomas B. Croat, principal investigator).

[2] The treatment for this family was coordinated by W. G. D'Arcy, Missouri Botanical Garden, who also wrote the introductory material including family description, discussion of morphology, conspectus of the family, and key to the genera. Authorship for tribes or subtribes is indicated at the beginning of the taxon. Except for editorial decisions agreed upon in the interest of uniformity of terminology and format, each author is solely responsible for his treatment.

ANN. MISSOURI BOT. GARD. 62: 835–1322. 1975.

from the inner (disc) florets, often with a straplike, entire, or denticulate corolla (ligule), the androecium usually wanting, the style branches 2, mostly slender, glabrate, the ovary fertile or not, sometimes 3-angled; inner (disc) florets mostly with tubular, variously expanded, 4–5-lobed corollas, sometimes somewhat zygomorphic, the anthers mostly oblong, marginally connate, introrse with sterile tips, basally blunt or tailed, the style branches 2, pubescent, glabrate or glandular, the ovary terete or compressed, often with an apical nectary. *Fruit* usually an achene, rarely baccate or drupaceous, or a utricle formed by fusion of the achene with paleas, bracts or other parts, the pericarp mostly hard; pappus usually present, of bristles, awns, or scales; sometimes with a distinct carpopodium.

The Compositae vies with the Orchidaceae and Gramineae as the largest vascular plant family, with some 30,000 species and over 1,000 genera. It is also one of the most easily recognized and widespread of flowering plant groups. The family is well represented in temperate regions with large numbers of species in most dry areas. In the New World, diversity is especially great in Mexico and Peru, and upland Panama hosts many species related to groups from these regions. In the lowlands there are many widespread weeds. Many species from the forests have been recently elucidated.

In Panama the tribes Eupatorieae and Heliantheae together constitute more than half the species present. The Eupatorieae includes many species with special adaptations such as epiphytism, scandent habit, and perhaps tolerance to shade that permit survival in forests. A number of species are trees. The tribe is mainly New World in distribution. Of the 83 Panamanian species, 24 are now known as endemics. Panamanian members of the Heliantheae are often widespread weeds of disturbed or open situations and many derive from groups better represented in Mexico.

Although contiguous with other countries having a rich development of Compositae, Panama is not always a corridor in a continuum of species linking neighboring areas. For example, 37 species of *Baccharis* have been reported for Colombia but only 2 are known in Panama, and Gibson (personal communication) has identified 20 species of *Vernonia* in Guatemala but only 6 species are known in Panama.

In spite of its large number of species and widespread occurrence, members of this family are of relatively little economic importance. In Panama a number of species are cultivated for ornament and some of these are sold as cut flowers in markets. *Pluchea carolinensis* (salvia) is widely cultivated as a medicinal, and *Lactuca sativa* (lettuce) is grown for salads. Many species are noxious weeds of cultivation and pastures.

The major tribal categories in the Compositae are fairly well agreed upon with the majority of workers accepting 12 or 13 tribes. There is some disagreement as to the placement of particular genera, and proposals have recently appeared (e.g., Robinson & Brettell, 1973a, 1973b, 1973c) to base distinct tribes on some of the genera of anomalous placement. The genus *Liabum* is here treated with the Senecioneae, *Isocarpha* with the Eupatorieae, *Schistocarpha* with the Senecioneae, and *Trichospira* with the Heliantheae. *Jaegeria* and *Sabazia* are treated in subtribe Galinsoginae of the Heliantheae instead of in subtribe Helianthinae where they

have often been placed. The traditional tribe Helenieae has long been subject to question, and genera occurring in Panama which were earlier referred to the Helenieae are treated here in the Tribe Tageteae. They are not closely related to other genera usually placed in the Helenieae and they are perhaps not closely related to other tribes.

No tribe can be considered ancestral to the rest of the family but several tribes have been proposed as primitive stocks: Vernonieae (Augier & Du Merac, 1951), Senecioneae (Small, 1917–1919), Heliantheae (Cronquist, 1955), and Cardueae (Leonhardt, 1949).

The 13 tribes commonly recognized in the family are often identified by the Roman numerals used by Bentham (1873a) and are employed here. Tribes IX (Calenduleae) and X (Arctoteae) do not occur in Panama. The arrangement of Panamanian genera into tribes is indicated in the following conspectus. The characters employed are merely synoptical and should not be relied upon for the determination of plants. An artificial key to genera follows. Each tribe is provided with a separate key to its constituent genera.

Chromosome numbers cited in the text are reported either in literature indicated or in the series of general compilations (Cave, 1956–1964; Darlington & Janaki Ammal, 1945; Darlington & Wylie, 1955; Keil & Stuessy, 1975; Moore, 1968–1970; Ornduff, 1965–1967; Powell & Turner, 1963; Turner & King, 1964; Turner & Flyr, 1966).

REED, cited occasionally as repository for plant specimens, indicates the private herbarium of Clyde F. Reed, 10105 Harford Rd., Baltimore, Md. U.S.A.

Unless otherwise indicated, all illustrations are of Panamanian collections.

Morphology

Plants of the Compositae display a range of specialized morphology not found in other families, and terminology is often particular to the family. A hand lens or dissecting microscope is useful in examining these plants and some features must be studied with a compound microscope. Literature citations in the following survey of terminology refer mainly to good illustrations of Compositae structures.

Pubescence and glands.—Characteristic hair (trichome) types (Fig. 1) are found in several groups of Compositae. In the Vernonieae hairs are sometimes sturdy, elongate and single-celled. In the Eupatorieae and Astereae hairs are usually many-celled and uniseriate or moniliform, with the basal or apical cell sometimes slightly differentiated. Arachnoid hairs, too fine to be seen in cellular detail under magnifications less than ×45, occur and may form tomentum in the Inuleae, Senecioneae, and Cardueae. A specialized "verrucose hair" occurs in many genera of the Heliantheae. This hair consists of a multicellular basal rosette, one or two sturdy, distinctly verrucose, erect cells and an apex of one or two smooth, acicular cells. The basal rosette of cells is sometimes calcified giving the leaf a punctate appearance, and the sometimes calcified rugose and apical cells may result in a scabrous leaf surface. Large multiseriate hairs occurring in *Trixis*, *Hieracium*, *Pectis*, etc. may be termed bristles. Branched hairs occur on *Hieracium*. For a discussion of the double hairs (Zwillingshaare) found on the ovaries of many genera and especially of some primitive elements see Hess (1938).

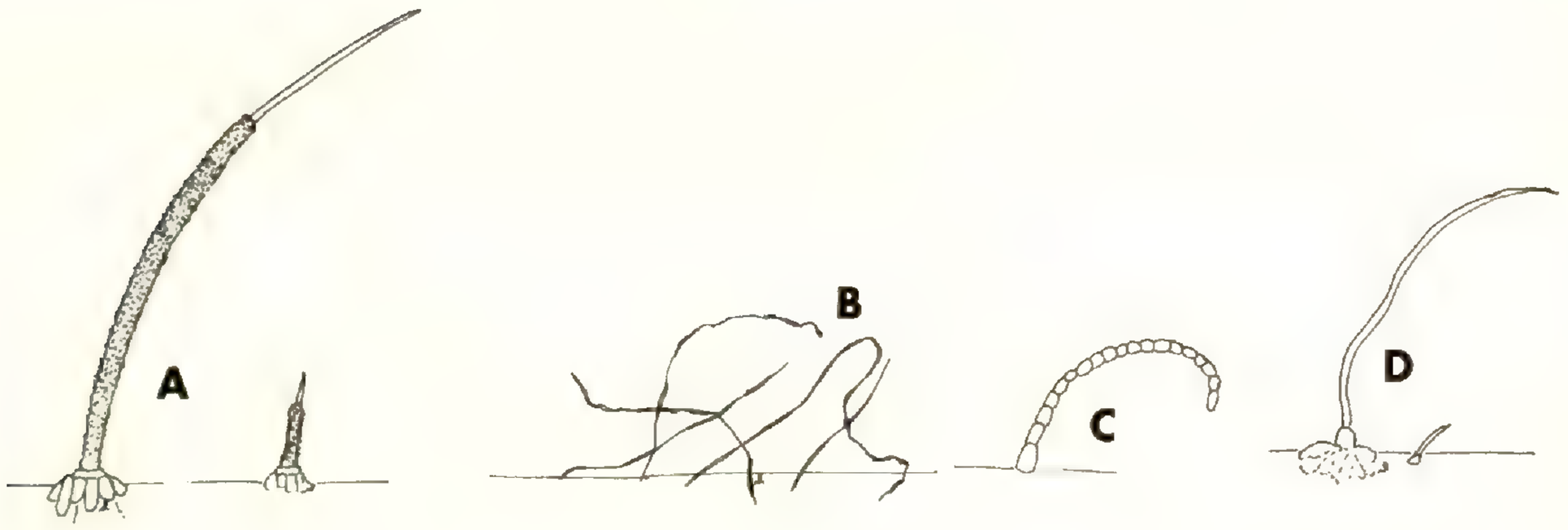

FIGURE 1. Commonly used diagnostic characters in Compositae.—A–D. Hair on leaves.—A. Verrucose hairs of Heliantheae, *Wedelia calycina*. [After *Tyson 6624* (MO).]—B. Arachnoid hairs, *Gnaphalium americanum*. [After *Croat & Porter 15619* (MO).]—C. Uniseriate, moniliform hair, *Fleischmannia pratensis*. [After *D'Arcy & D'Arcy 6335* (MO).]—D. Long unicellular hair in Vernonieae, *Pseudelephantopus spicatus*. [After *Croat 4168* (MO).]—E–I. Stamens in dorsal view. Note apical appendages, anther bases, and anther collars (arrow).—E. Anther bases obtuse, *Fleischmannia pratensis*. [After *D'Arcy & D'Arcy 6335* (MO).]—F. Anther bases sagittate, auricles united, *Taraxacum officinale*. [After *D'Arcy & D'Arcy 6459* (MO).]—G. Anthers sagittate with crumpled tails, *Pterocaulon virgatum*. [After *Allen 1325* (MO).]—H. Anthers tailed (fimbriate), *Gnaphalium americanum*. [After *Croat & Porter 15619* (MO).]—I. Anther tails with hairs, anther appendages not demarcated, *Onoseris onoserioides*. [After *Croat 22223* (MO).]—J–N. Style branches.—J. Lactucoid type, *Taraxacum officinale*. [After *D'Arcy & D'Arcy 6459* (MO).]—K. Vernonioid type, *Vernonia canescens*. [After *Croat 8686* (MO).]—L. Eupatorioid type, *Fleischmannia pratensis*. [After *D'Arcy & D'Arcy 6335* (MO).]—M. Carduoid type, *Cirsium mexicanum*. [After *Busey 541* (MO).]—N. Senecioid type approaching Helianthaeoid type. Note truncate, penicellate apex and rudimentary appendage, *Senecio megaphyllus*. [After *Webster et al. 17222* (MO).]

Conspicuous, often pellucid oil glands of various shapes are arranged characteristically on leaves and involucres in the Tageteae (Figs. 90, 93). In *Sigesbeckia* (Fig. 70), *Hieracium* (Fig. 107), and *Sonchus* (Fig. 109), large globose glands are displayed on bristles. In *Baccharis*, a coating of glandular material may make the leaf shiny. With the aid of a lens, punctate glands in the leaf surface or globose glandular materials on the surface may be observed in many species. Laticifers, completely internal to the epidermis, are visible with effort as irregular areas of differentiated surface in the leaves of *Critonia daleoides*. The sap of this species is clear. In the Lactuceae a network of laticifers invisible without special techniques yields copious milky sap.

Leaf arrangement.—In Panama leaves are opposite or rarely verticillate in most Eupatorieae, Tageteae, many Heliantheae, and in *Liabum* and *Schistocarpha* (both Senecioneae), but are alternate in all other groups. Plants with leaves in basal rosettes belong to groups with alternate leaves. In plants with opposite leaves, it is not unusual for some leaves and branches in the region of the inflorescence to be alternate. The converse obtains in *Trichospira* where leaves in the inflorescence are opposite and in the rest of the plant alternate. Both *Verbesina* and *Ambrosia* are known in Panama only by alternate-leaved species but opposite-leaved species occur in nearby countries. *Decachaeta* is the only genus in the Eupatorieae with entirely alternate leaves.

Involucral bracts (phyllaries).—These are mostly numerous and in most groups are overlapping in several graded series. Except in the Eupatorieae this is referred to as imbricate, but in the Eupatorieae the terms eximbricate, subimbricate, and imbricate are used to refer to degrees of overlapping. Good examples of these conditions are *Ageratina anisochroma* (Fig. 12), *Bartlettina* (Fig. 16), and *Chromolaena odorata* (Fig. 18), respectively. In some species of Tageteae, Senecioneae, Mutisieae, and Lactuceae the bracts do not overlap but are valvate, touching only at the margins (Fig. 110), or they may sometimes be marginally connate for part of their length. A whorl of short bracts at the base of the involucre (Fig. 110) may be referred to as either outer involucral bracts or as calyculate bracts. Commonly one or more subinvolucral bracts may be found on the pedicel, sometimes in a different phyllotaxy from the rest of the plant. In the Elephantopodinae the involucral bracts are decussate, and in these genera with their heads fused into a common receptacle, a series of subinvolucral bracts (Fig. 10) forms a pseudoreceptacle around the glomerule.

Paleas (chaff) and receptacle (torus).—Convention refers to bracts external to the outermost whorl of florets as involucral bracts and those internal to it as paleas. Although artificial, this distinction causes little difficulty. The two structures are homologous with leaves but the paleas are usually considerably more modified. Paleas are best developed in the Heliantheae and Mutisieae but isolated species or genera of the Eupatorieae, Astereae, Senecioneae, and Lactuceae and perhaps other tribes also have paleas. In the Heliantheae the paleas frequently enfold the ovary (Fig. 53c, 76c) and may be bent over the corolla in bud or occasionally are apically modified into awns or cusps. The paleas of *Eclipta*, *Cirsium* and *Liabum* are narrowed into bristles or awns. In many genera paleas are reduced to hairs or low scales which may persist on the

receptacle. In some genera, low hairs or spicules on the receptacle are referred to as paleas although they may consist of enations of the receptacle, or remains of carpopodia and are not homologous with the bracts noted above. Aged receptacles may be fimbrillate (fringed), pilose, foveate (pitted), verrucose (warty or knobby), alveolate (honeycombed), spiculiferous, muricate (spiny), or naked (lacking paleas). The receptacle tissue may be completely sclerified or include parenchyma.

Corollas.—Corollas (Hoffman 1894: 99, 101; Solbrig 1963b: 451; Bentham 1873b: tab. 8) are considered to be either ligulate (rays) or tubular (disc), although the tubular form includes modifications to campanulate, funnelform, etc., and ligulate corollas usually consist of a tube and a straplike ligule. When extremely narrow, corollas are termed filiform or capillary (Fig. 34E). The outline made by the top of the corollas and paleas is referred to as the disc. In the Lactuceae all corollas have a 5-lobed ligule. In other groups, ligulate corollas are confined to the outer whorls of florets on the head or are lacking. In the Mutisieae (Figs. 104, 106), ligulate corollas have a 4-lobed ligule and a short, opposing lobe at the top of the tube (bilabiate). In the Astereae, Inuleae, Heliantheae, Tageteae, Senecioneae and Anthemidae, ligules are 2–3-lobed or entire (Figs. 34B, 48B, 81A, 93B, 98B), and an opposing lobe is seldom present. In *Zinnia* (Fig. 58C) and *Heliopsis* (Fig. 57C) (Heliantheae) the corolla consists of a ligule persistent on the achene and a tube is lacking, and in *Melampodium* also the tube may be obsolete. Ligulate corollas are lacking in all Panamanian taxa of Vernonieae, Eupatorieae, and Cardueae and only tubular corollas are present. Tubular corollas consist of a basal tube, an expanded limb, and 4–5 apical lobes. They are mostly actinomorphic but sometimes one suture of the limb is deeper than the others and in other cases two sutures are deeper, producing slightly bilabiate corollas. In the Eupatorieae attention has been drawn to the systematic importance of cell outline in the corolla lobes; bulging cells can often be seen at ×10–×50 magnifications but sinuous walls are visible only under a compound microscope after the special preparation of the tissue described by King & Robinson (1970).

Sexual condition.—Sexual condition of the florets is of great systematic utility. In the Vernonieae, Eupatorieae, and Cardueae (Panama) and in a few genera in other groups, all florets are alike, perfect, and have tubular corollas. Such heads are termed discoid. All florets of the Lactuceae are also perfect and have only ligulate corollas. These heads are termed ligulate. In the above mentioned groups all florets are fertile, producing mostly viable achenes. In most other groups, the outer florets are pistillate, lack stamens, and only rarely produce staminodes. The outer florets may have tubular or ligulate corollas and the heads are termed radiate or disciform depending on whether the ligules are elongate (exceeding the stigmas and pappus) or short and inconspicuous. The ovaries may be fertile or sterile. Florets toward the center of such heads are morphologically perfect with tubular corollas and functional stamens. The ovaries may be fertile or sterile. Variations in the above conditions occur in a few groups. Some Mutisieae have two peripheral whorls of pistillate florets, the outer with ligulate corollas and the inner with tubular corollas. Whorls internal to these have perfect florets with

tubular corollas. In a few cultivated plants, e.g., some strains of *Dahlia*, *Chrysanthemum*, and *Tagetes*, proliferation of pistillate, often abortive, florets with ligulate corollas may supplant normal florets with tubular corollas.

Stamens.—Stamens (Fig. 1, Hoffman, 1894: 104; Bentham, 1873b: tab. 9) are usually of the same number as the corolla lobes. Filaments are usually compressed and the anthers are connate or coherent into a narrow tube. The anther apex is usually sterile and differentiated into a distinct, hyaline appendage. In *Piquiera*, *Eclipta*, and *Eleutheranthera* the appendage is much reduced or wanting. In the Mutisieae and in *Youngia* (Lactuceae) the anther apex is sterile but not demarcated on the dorsal (outer) side, appearing as a homogeneous continuation of the thecas. Anther bases may be blunt, auriculate, sagittate, or with variously elaborated tails. The auricles of adjacent anthers are sometimes united. In some cases short auricles appear to be derived from longer but crumpled tails. Tails are present in most taxa of Inuleae and Mutisieae. The order in which tribes are usually treated roughly follows the degree of elaboration of the anther bases.

A ring or region of specialized cells near the top of the filaments, the anther collar (Figs. 1, 12–33), acts as a hinge to permit straightening of the filaments at anthesis when the style pushes through the anther tube with much of the pollen. Characteristics of the anther collar have been used systematically in the Eupatorieae and Senecioneae. Exothecial cells of the anthers, visible under a compound microscope after special preparation, have also been of systematic use in the Eupatorieae (King & Robinson, 1970).

Styles.—The style (Hoffman, 1894: 107, 109, 110; Bentham 1873b: tab. 10; Solbrig, 1963b: 443; Gleason, 1952: 324) is typically a 2-branched shaft which may have an expansion (node) near the base (Figs. 12D, 75E). The basal expansion occasionally acts as a nectary and sometimes it is stipitate above the ovary by a slender pedicel. The base of the shaft is frequently immersed in a cupular nectary on the ovary apex (Fig. 34). In some species the branches do not separate and the shaft is entire. In most cases the dorsal (abaxial) surface is pubescent and the ventral (adaxial) surface is more or less flat. The stigmatic region is on the edge or ventral surface in a configuration characteristic of the tribe. Not always correlated with stigmatic position, several shapes of style branch are common (Fig. 1):

Lactucoid: Branches slender, longitudinally uniform, and sparingly pubescent. The apex is acute or obtuse. This type occurs in the Lactuceae and in pistillate florets of other tribes.

Vernonioid: Branches elongate, longitudinally uniform, and often copiously pubescent. This type occurs in the Vernonieae.

Eupatorioid: Branches elongate, gradually expanded near the apex, minutely pubescent, papillose, or smooth. It is stigmatic at the margins near the base, and distal portions of the branches may be referred to as appendages. This type occurs in only the Eupatorieae (Figs. 11–33).

Senecioid: Branches often short, truncate, the apex with a fringe of papillae or hairs (penicillate). This type occurs in some species of Senecioneae, Anthemideae, and Inuleae.

Helianthoid: Branches are short, pilose near the apex, and sometimes with a

triangular or filiform appendage at the tip. This type occurs in several genera of Astereae, Inuleae, and Heliantheae (Fig. 54C), and intergrades with the Senecioid type.

Carduoid: Branches short and smooth, the shaft has an annulus of hairs or thickening near the apex. The type occurs in the Cardueae.

Ovaries.—Taxonomic characters of the ovary are usually expressed in terms of the achene, and younger stages may be misleading. Wings in some *Verbesina* species do not develop until after anthesis, while in *Wulffia* the awn (pappus) is deciduous soon after anthesis. In many groups a cupular nectary (Figs. 33E, 75D, E) is present at the apex of the ovary and in some genera, e.g., *Ayapana*, it is conspicuous. This is distinct from the expanded style base which resembles a nectary in some groups (Figs. 12D, 75E). The nectary may be stipitate. It may envelop the basal enlargement of the style shaft or end below it, in which case the stylar expansion appears stipitate. The nectary and style shaft are adnate only at the base. In several tribes; Vernonieae, Eupatorieae, Inuleae, Tageteae, and Anthemideae, the ovaries are characteristically terete, often ribbed, while in the Astereae and Heliantheae they are often compressed laterally (radially) or dorsiventrally (tangentially).

Fruits.—The usual dispersal unit in the Compositae is the achene, which consists of pericarp, endosperm and embryo, and sometimes includes a pappus, persistent nectary, and carpopodium. The pericarp (rind) is usually hard but is soft and fleshy in *Wulffia*. The exocarp is sometimes transparent. The achene may be apically narrowed into a beak (Fig. 108) which subtends the pappus, and the top of the beak may be expanded in a flange (Fig. 108). All structures surmounting the achene except the nectary are referred to as pappus. This may consist of hairs, bristles, scales (squamellae), awns or rarely glands, and sometimes these elements are fused in a corona or annulus (Fig. 66). Bristles or hairs are usually strigulose (barbellate, scabrid) and are especially fine and numerous in the Senecioneae and Lactuceae. Stout bristles are sometimes basally flattened or expanded. Scales may be lacerate (Fig. 9C). In the Heliantheae awns are common. While the pappus is of great utility in identifying Compositae, it is not unusual to find epappose (calvous) achenes in individuals or species of normally pappose groups. The carpopodium (hypophyses) is sometimes conspicuous (Figs. 19E, 106C), and the cellular arrangement has been given taxonomic weight in the Eupatorieae. A stipe arising above the carpopodium occurs in some species of *Verbesina*. In *Unxia* (Fig. 54) a notch appears on the achene at the carpopodium site.

Frequently, the achene is united with enveloping bracts or paleas or with adjacent florets, and the compound structure falls together. This compound fruit may be termed a utricle in the same sense as the term is used in the Chenopodiaceae and Urticaceae. It has also been known as an involucral fruit or fruiting involucre. The utricle may be flat and winglike or samaroid as in *Delila* (Fig. 45), covered with hooks or spines and burlike as in *Acanthospermum* (Fig. 47), or the bract may be tightly fused to and hardly distinguishable from the achene as in *Melampodium* (Fig. 52). In *Sclerocarpus* (Fig. 69) the surrounding bract is adnate to the achene apex but sometimes breaks free during dispersal.

Several achenes (or heads) may be held in glomerules with associated bracts to form a burlike utricle in members of the Vernonieae (Fig. 10B).

In a number of Panamanian Compositae the fruit is fleshy and bird-dispersed. The inulin-rich pericarp of *Wulffia* is soft and fleshy and this baccate fruit is technically a drupe. In *Clibadium* and *Milleria* (Fig. 46) parts of the involucre are fleshy or even juicy and form a baccate structure. The baccate condition is best noted in fresh material and may pass unnoticed when dry.

Achene shape is sometimes indicative of tribe; thus the Heliantheae and Cardueae have generally larger achenes than those of other tribes and in the Lactuceae, Tageteae, and Mutisieae, fruits are often long and thin. Achenes are often compressed in the Astereae and Heliantheae and sometimes in the Lactuceae, but are mostly oblong and cylindrical in the Vernonieae, Eupatorieae, Inuleae, and Senecioneae. Winged achenes occur only in the Heliantheae.

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Much literature in the text is listed either with the appropriate genera, or if the same citation occurs in two different genera, its reference will be found here.

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Conspectus of the Panamanian Compositae[3]

a. Heads with staminate or perfect florets towards the middle, the corollas tubular, 5-lobed; sometimes with pistillate florets towards the outside, the corollas tubular or ligulate; sap not milky.
  b. Anther tips with sterile, tonguelike, often hyaline appendages.
    c. Florets all alike, perfect, corollas tubular, not yellow; anthers not tailed; receptacle naked.
      d. Leaves alternate; style branches slender, terete, hairy all over, the style shaft apically hairy; anthers auricled; hairs often 1-celled ---------- Tribe I. Vernonieae p. 856
        e. Heads all distinct ---------- Subtribe A. Vernoniinae
          1. *Centratherum*
          2. *Piptocarpha*
          3. *Pollalesta*
          4. *Struchium*
          5. *Vernonia*
        ee. Heads fused in glomerules in a common receptacle ---------- Subtribe B. Elephantopodinae
          6. *Elephantopus*
          7. *Pseudelephantopus*
          8. *Rolandra*
          9. *Spiracantha*
      dd. Leaves mostly opposite (except sometimes in the region of the inflorescence); style branches gradually expanded near the tips, papillose or short-hairy, the style shaft often glabrous; anthers obtuse or rounded; hairs multicellular, often moniliform ---------- Tribe II. Eupatorieae p. 888
        10. *Adenostemma*
        11. *Ageratina*
        12. *Ageratum*
        13. *Austroeupatorium*
        14. *Ayapana*
        15. *Bartlettina*
        16. *Brickellia*
        17. *Chromolaena*
        18. *Condylidium*
        19. *Critonia*
        20. *Decachaeta*
        21. *Fleischmannia*
        22. *Gongrostylus*
        23. *Hebeclinium*
        24. *Heterocondylus*
        25. *Isocarpha*
        26. *Koanophyllon*
        27. *Mikania*
        28. *Neomirandea*
        29. *Piqueria*
        30. *Sciadocephala*
        31. *Stevia*
        32. *Tuberostylis*
    cc. Florets often not all alike, corollas often yellow; anthers sometimes tailed; receptacle naked or with paleas.
      f. Leaves mostly not spiny; involucral bracts not spiny; anthers tailed or not; style shaft without an apical ring.
        g. Leaves alternate; style branches flattened-fusiform, sometimes apically appendaged or rounded; anthers tailed or not; receptacle mostly naked; pappus mostly of bristles.
          h. Anthers obtuse; style branches often appendaged; achene often compressed; hairs multicellular ---------- Tribe III. Astereae p. 1004
            33. *Archibaccharis*
            34. *Aster*
            35. *Baccharis*
            36. *Conyza*
            37. *Erigeron*
            38. *Lagenifera*
          hh. Anthers tailed; style branches rounded; achene plump; hairs arachnoid ---------- Tribe IV. Inuleae p. 1033
            39. *Blumea*
            40. *Gnaphalium*
            41. *Helichrysum*
            42. *Pluchea*
            43. *Pterocaulon*
            44. *Tessaria*
        gg. Leaves alternate or opposite; style branches flattened-fusiform, sometimes apically appendaged; anthers not tailed; receptacle with paleas or naked; pappus of bristles, awns, or scales.
          i. Pappus of awns, stiff bristles, or scales; style branches often appendaged.
            j. Involucre without transparent margins; leaves mostly opposite, often 3-nerved from the base or trifoliolate.
              k. Receptacle mostly with paleas enfolding the achenes; involucral bracts mostly unequal, overlapping; leaves mostly eglandular; hairs often verrucose ---------- Tribe V. Heliantheae p. 1053
              l.′ Florets few; central florets abortive; receptacle naked ---------- Subtribe A. Milleriinae
                45. *Delilia*
                46. *Milleria*

[3] Adapted in part from Bentham (1873a).

l.″ Florets many; central florets abortive; receptacle mostly with paleas ---------- Subtribe B. Melampodiinae

47. *Acanthospermum*
48. *Baltimora*
49. *Clibadium*
50. *Ichthyothere*
51. *Melampodium*
52. *Polymnia*
53. *Unxia*

l.‴ Heads discoid and unisexual, or radiate and central florets abortive ---------- Subtribe C. Ambrosiinae

54. *Ambrosia*
55. *Parthenium*

l.⁗ Heads radiate, the corollas of the ray florets without a tube, persistent ---------- Subtribe D. Zinniinae

56. *Heliopsis*
57. *Zinnia*

l.⁗′ Achenes laterally compressed; pappus often of awns ---------- Subtribe E. Helianthinae

58. *Eclipta*
59. *Eleutheranthera*
60. *Garcilassa*
61. *Lasianthaea*
62. *Melanthera*
63. *Montanoa*
64. *Oyedaea*
65. *Rumfordia*
66. *Salmea*
67. *Sclerocarpus*
68. *Sigesbeckia*
69. *Simsia*
70. *Spilanthes*
71. *Tithonia*
72. *Verbesina*
73. *Viguiera*
74. *Wedelia*
75. *Wulffia*
76. *Zexmenia*

l.⁗″ Achenes dorsiventrally compressed; involucral bracts biseriate ---------- Subtribe F. Coreopsidinae

77. *Bidens*
78. *Chrysanthellum*
79. *Cosmos*
80. *Dahlia*
81. *Hidalgoa*
82. *Synedrella*
83. *Trichospira*

l.⁗‴ Pappus of plumose awns or bristles ---- Subtribe G. Galinsoginae

84. *Calea*
85. *Galinsoga*
86. *Jaegeria*
87. *Sabazia*
88. *Tridax*

kk. Receptacle naked; involucral bracts equal, mostly valvate; leaves with oil glands; glabrate ---------- Tribe VI. Tageteae p. 1220

89. *Dyssodia*
90. *Pectis*
91. *Porophyllum*
92. *Tagetes*

jj. Involucre with hyaline, transparent, brownish margins; leaves alternate, with a strong midvein ---------- Tribe VII. Anthemideae p. 1241

93. *Chrysanthemum*

ii. Pappus of soft, silky, hairlike bristles; style branches not appendaged ---------- Tribe VIII. Senecioneae p. 1244

94. *Emilia*
95. *Erechtites*
96. *Liabum*
97. *Neurolaena*
98. *Schistocarpha*
99. *Senecio*

ff. Leaves and involucral bracts spiny; anthers tailed; style shaft with an apical ring ---------- Tribe XI. Cardueae p. 1272

100. *Cirsium*

bb. Anther tips sterile but not differentiated into hyaline, tonguelike appendages; anthers mostly tailed ---------- Tribe XII. Mutisieae p. 1276

101. *Chaptalia*
102. *Gerbera*
103. *Jungia*
104. *Lycoseris*
105. *Onoseris*
106. *Trixis*

aa. Heads with only perfect florets, the corollas ligulate, 5-denticulate; sap milky ---------- Tribe XIII. Lactuceae p. 1292

107. *Hieracium*
108. *Hypochoeris*
109. *Sonchus*
110. *Taraxacum*
111. *Youngia*

Key to the Genera

1. Leaves opposite (reduced leaves or bracts sometimes alternate near the inflorescence).
  2. Leaves compound or deeply lobed.
    3. Leaves and involucre with conspicuous oil glands ..... 92. *Tagetes*
    3.′ Leaves and involucre without glands.
      4. Leaves simple with pointed lobes; achene subglobose or prismatic; pappus of fine bristles or wanting.
        5. Achenes subglobose; pappus wanting ..... 52. *Polymnia*
        5.′ Achenes oblong, prismatic, or 5-ribbed; pappus of bristles.
          6. Pappus bristles fine, strigose; achene glabrous or pubescent; trees or shrubs; paleas absent ..... 28. *Neomirandea*
          6.′ Pappus bristles basally flattened or stout, plumose; achene copiously ascending-pilose; paleas present ..... 88. *Tridax*
      4.′ Leaves compound or if simple the lobes rounded; achene linear or compressed; pappus of barbed awns or wanting.
        7. Heads large, the involucre more than 1 cm across; inner involucral bracts with broad, hyaline margins; trees or cultivated herbs ..... 80. *Dahlia*
        7.′ Heads smaller, the involucre mostly less than 1 cm across; involucral bracts with herbaceous margins; herbs, sometimes cultivated.
          8. Vines climbing by hooked petioles; achene oblong; outer involucral bracts 5, slender, spreading ..... 81. *Hidalgoa*
          8.′ Herbs or vines lacking hooked petioles; achene linear; outer involucral bracts various.
            9. Achene with a distinct beak; leaves deeply dissected, more than 3 cm long ..... 79. *Cosmos*
            9.′ Achene without a distinct beak; leaves trifoliolate, or less than 3 cm long ..... 77. *Bidens*
  2.′ Leaves simple, not deeply lobed.
    10. Fruit a simple, dry achene, not spiny, falling free from the head and involucral parts.
      11. Pappus of 1–5 stalked knobs.
        12. Corolla pilose near the lobes; heads with more than 10 florets; involucral bracts 10–20; anther appendages wider than long ..... 10. *Adenostemma*
        12.′ Corolla generally puberulent outside; heads usually with fewer than 10 florets; involucral bracts 7–8; anther appendages longer than wide ..... 30. *Sciadocephala*
      11.′ Pappus of bristles, scales, awns, or wanting, not of stalked knobs.
        13. Pappus of numerous (more than 10) bristles or scales; paleas mostly wanting.
          14. Involucral bracts fewer than 10.
            15. Heads discoid; florets all alike, all with stamens.
              16. Heads more than 15 mm tall, with 5 involucral bracts and numerous florets ..... 91. *Porophyllum*
              16.′ Heads less than 10 mm tall, with 4 involucral bracts and 4 florets ..... 27. *Mikania*
            15.′ Heads radiate; outer florets lacking stamens ..... 90. *Pectis*
          14.′ Involucral bracts more than 10.
            17. Involucral bracts 10–15 mm tall, oblong, blunt, with conspicuous dark, glandular streaks ..... 89. *Dyssodia*
            17.′ Involucral bracts not as above.
              18. Pappus plumose, the bristles (scales) basally broad ..... 88. *Tridax*
              18.′ Pappus not plumose (sometimes strigulose or barbellate).
                19. Leaves strongly discolorous, green or brown and glabrate above, whitish, sometimes tomentose, beneath.
                  20. Florets yellow or white; leaves broad, felty-tomentose beneath ..... 96. *Liabum*
                  20.′ Florets violet or white; leaves narrow, glabrous beneath.
                    21. Principal leaves more than 5 cm long; involucre manifestly pubescent; corolla tube slender, strongly expanded about halfway up ..... 11. *Ageratina*
                    21.′ Principal leaves less than 5 cm long; involucre glabrate; corolla gradually broadening upward ..... 12. *Ageratum*
                19.′ Leaves concolorous, similar on both sides.

22. Receptacles paleaceous; corollas yellow or white; verrucose hairs often present.
23. Pappus bristles basally flat and broad; achenes pubescent ..... 84. *Calea*
23.′ Pappus bristles slender; achenes glabrous ..... 98. *Schistocarpha*
22.′ Receptacles naked; corollas white, pink, purplish, not yellow; hairs not of verrucose type, mostly moniliform.
24. Heads with fewer than 6 florets.
25. Leaves copiously glandular beneath; small herbs ..... 18. *Condylidium*
25.′ Leaves eglandular beneath; shrubs ..... 19. *Critonia*
24.′ Heads with more than 6 florets.
26. All involucral bracts deciduous in age; involucre tubular, 5–8 mm tall, 2–3 times longer than broad, the bracts appressed, overlapping, the tips of the outermost differentiated and appearing as brown or green spots on the yellowish, striate involucre ..... 17. *Chromolaena*
26.′ At least some involucral bracts persistent; involucre not as above.
27. Anther appendages shorter than wide, often inconspicuous.
28. Style branches with prominent, fusiform knobs at the tips; outer involucral bracts with more than 7 fine, elevated ribs; inner involucral bracts more than twice as long as the achene; vines ..... 22. *Gongrostylus*
28.′ Style branches sometimes expanded apically but without knobs (expansion in only 2 dimensions); outer involucral bracts without fine, elevated ribs; inner involucral bracts only slightly exceeding the achene; herbs or shrubs ..... 26. *Koanophyllon*
27.′ Anther appendages as long as wide or longer, mostly prominent.
29. Pedicels glabrous; involucral bracts narrow with broad, hyaline margins, glabrous; achene weakly 10-ribbed ..... 16. *Brickellia*
29.′ Pedicels and inflorescence branches pubescent, mostly tomentose; involucral bracts mostly not as above; achene 2–6-ribbed.
30. Corolla slender, strongly expanded about halfway up; pappus bristles easily deciduous ..... 11. *Ageratina*
30.′ Corolla gradually expanded upwards, the limb not sharply demarcated; pappus bristles persistent.
31. Heads large; involucral bracts more than 2 mm wide; receptacle more than 2 mm across; achenes more than 2.2 mm long.
32. Pedicels stout; achenes more than 2.5 mm long ..... 24. *Heterocondylus*
32.′ Pedicels slender; achenes less than 2.5 mm long ..... 15. *Bartlettina*
31.′ Heads smaller; involucral bracts less than 2 mm wide; receptacle less than 2 mm across; achenes mostly less than 2.2 mm long.
33. Most leaves less than 6 cm long (excluding petiole) ..... 21. *Fleischmannia*
33.′ Leaves more than 6 cm long.
34. Receptacle hemispherical, hairy; corolla lobes pilose ..... 23. *Hebeclinium*
34.′ Receptacle flat or weakly convex, glabrous; corolla lobes glabrous or pilose.
35. Leaves subsessile, the blade expanded abruptly (not always widely) above the short petiole; nectary large and conspicuous on the achene apex ..... 14. *Ayapana*

35.′ Leaves petiolate, the blade basally acuminate; nectary mostly not prominent.
36. Involucral bracts 1 mm wide or less ..... 21. *Fleischmannia*
36.′ Involucral bracts 1–2 mm wide.
37. Leaves copiously pubescent above; achene glandular ... 13. *Austroeupatorium*
37.′ Leaves glabrate above; achene eglandular.
38. Corolla lobes pilose; heads with more than 20 florets ..... 15. *Bartlettina*
38.′ Corolla lobes glabrous; heads with 8–12 florets ..... 19. *Critonia*
13.′ Pappus of fewer than 8 bristles, scales, awns, or wanting; paleas mostly present.
39. Leaves copiously glandular beneath.
40. Heads radiate; florets bright yellow.
41. Large herbs or shrubs; leaves broad, pubescent; paleas conspicuous ..... 63. *Montanoa*
41.′ Small herbs; leaves narrow, glabrate; paleas wanting ..... 90. *Pectis*
40.′ Heads discoid; florets white or purplish.
42. Heads with 3–5 perfect florets; involucral bracts 3–5 ..... 31. *Stevia*
42.′ Heads with more than 5 florets; involucral bracts 5.
43. Involucre longer than the disc; florets fewer than 12 ..... 59. *Eleutheranthera*
43.′ Involucre shorter than the disc; florets mostly more than 12.
44. Heads purplish; disc nearly flat; paleas wanting ..... 12. *Ageratum*
44.′ Heads whitish; disc strongly convex or conical; paleas present ..... 25. *Isocarpha*
39.′ Leaves eglandular beneath.
45. Outer involucral bracts 5, linear-spathulate, widely-spreading with conspicuous, stalked glands; verrucose hairs not present ..... 68. *Sigesbeckia*
45.′ Involucral bracts not as above; verrucose hairs often present.
46. Paleas linear, apically barbed ..... 58. *Eclipta*
46.′ Paleas broader or wanting, not apically barbed.
47. Heads discoid; florets all alike.
48. Achenes with 2–3 prominent, ciliate angles.
49. Heads solitary on long peduncles, sometimes in loose, ill-defined aggregates; heads more than 6 mm across ..... 70. *Spilanthes*
49.′ Heads in small, many-headed inflorescences; heads less than 6 mm across ..... 66. *Salmea*
48.′ Achenes terete, ribbed, or compressed, but not with 2–3 ciliate angles.
50. Heads with more than 15 involucral bracts; florets often more than 20.
51. Heads in well-defined inflorescences; paleas wanting.
52. Involucral bracts narrow, persistent; pedicels slender; erect, terrestrial plants ..... 12. *Ageratum*
52.′ Involucral bracts broad, the inner series deciduous; pedicels stout; epiphytes on mangroves ..... 32. *Tuberostylis*
51.′ Heads solitary or in loose, ill-defined aggregates; paleas present.
53. Achene compressed with definite angles; pappus of 2–8 caducous, strigose bristles; involucral bracts with blunt tips ..... 62. *Melanthera*
53.′ Achene mostly without definite angles; pappus of scales or wanting; involucral bracts with narrow tips ..... 73. *Viguiera*
50.′ Heads with fewer than 15 involucral bracts; florets mostly fewer than 15.
54. Pappus of two stout awns; leaves strongly discolorous, glabrous and drying dark above, grey tomentose beneath ..... 83. *Trichospira*

54.′ Pappus of low scales or wanting; leaves concolorous, pubescent or glabrate.
55. Paleas present; corollas evenly pubescent ..... 60. *Garcilassa*
55.′ Paleas wanting; corollas pilose on the tube, glabrate above ..... 29. *Piqueria*

47.′ Heads radiate; florets differentiated.
56. Achenes dimorphic, the innermost linear with 2(3) stout awns, the outermost flat with laciniate margins ..... 82. *Synedrella*
56.′ Achenes all alike, or if differentiated, the awns small and weak.
57. Heads small, less than 6 mm across; pappus mostly minute or wanting.
58. Herbs or shrubs more than 60 cm tall.
59. Heads white; heads in small clusters on pedicels mostly shorter than the heads; shrubs or large herbs.
60. Involucre biseriate; inflorescence of 10–30 heads ..... 50. *Ichthyothere*
60.′ Involucre multiseriate; inflorescence of 10–800 heads ..... 49. *Clibadium*
59.′ Heads yellow; heads mostly solitary on pedicels often much longer than the heads; tall herbs with slender branches ..... 48. *Baltimora*
58.′ Herbs less than 60 cm tall or sprawling.
61. Outer bracts short with prominent white margins; leaves narrowly spathulate, serrate near the apex ..... 78. *Chrysanthellum*
61.′ Outer bracts without white margins; leaves ovate or elliptical.
62. Petioles conspicuously long-pilose, the hairs eglandular; pedicels obscure, the heads subtended by a pair of large, foliaceous bracts; receptacle weakly convex ..... 53. *Unxia*
62.′ Petioles glabrate or if pilose, the hairs gland-tipped; pedicels evident, foliaceous bracts mostly wanting; receptacle conical or convex.
63. Achenes sharply 2–3-angled, conspicuously ciliate ..... 70. *Spilanthes*
63.′ Achenes eciliate, mostly plump, not angled.
64. Involucre with conspicuous, stout hairs; involucral bracts 1–2-seriate, narrow, but basally expanded; pedicel hairs eglandular ..... 86. *Jaegeria*
64.′ Involucre sparsely pilose; involucral bracts 2–many-seriate, broad, not basally expanded; pedicel hairs often gland-tipped.
65. Heads with 3–8 ray florets; florets each enclosed by an involucral bract and 2–3 paleas ..... 85. *Galinsoga*
65.′ Heads with 8–17 ray florets; florets not usually enclosed by involucral bracts ..... 87. *Sabazia*

57.′ Heads larger, more than 6 mm across; pappus mostly present.
66. Achene angles or wings ciliate, not pubescent overall.
67. Achene with prominent, sturdy awns, sometimes winged ..... 76. *Zexmenia*
67.′ Achene with weak, small awns or none, not winged ..... 70. *Spilanthes*
66.′ Achene not ciliate, sometimes minutely strigose.
68. Pappus of prominent, persistent awns; achene winged only apically or not at all.
69. Upper leaves alternate, most leaves lobed; heads large (involucre more than 2 cm across) ..... 71. *Tithonia*
69.′ All leaves opposite, not lobed; heads smaller.
70. Involucral bracts with slender, awnlike tips.
71. Achene sharply angled; ray florets fertile ..... 61. *Lasianthaea*

71.′ Achene only slightly angled; ray florets sterile ..... 73. *Viguiera*
70.′ Involucral bracts with blunt tips; ray florets sterile.
72. Achene evenly canescent or pilose with long hairs ..... 69. *Simsia*
72.′ Achene glabrate ..... 64. *Oyedaea*
68.′ Pappus various but not of prominent, persistent awns; if awns present, then the achene conspicuously winged.
73. Involucral bracts broadly rounded or truncate.
74. Achene smooth; corolla of the ray floret a sessile ligule (without a tube), persistent on the achene ... 57. *Zinnia*
74.′ Achene tuberculate (actually enfolded by an adnate involucral bract); corolla of the ray floret with a tube, falling before the achene matures ..... 51. *Melampodium*
73.′ Involucral bracts pointed.
75. Outer involucral bracts ca. 5, foliaceous, often wide-spreading from the base; corolla tube of ray florets elongate.
76. Ray florets fertile; corolla of disc florets without black hairs; achenes falling free; verrucose hairs wanting; inflorescence a panicle ..... 65. *Rumfordia*
76.′ Ray florets abortive; corolla of disc florets with black hairs near the apex; achenes enveloped by and falling with the palea; verrucose hairs present; inflorescence of solitary or loosely aggregated heads ..... 67. *Sclerocarpus*
75.′ Outer involucral bracts more than 5, not wide-spreading except sometimes at the tips; corolla tube of ray florets mostly shorter than the achenes or wanting.
77. Ray corolla lacking a tube, persistent on the achene; pappus wanting ..... 56. *Heliopsis*
77.′ Ray corolla with a tube, falling before the achene matures; pappus present or not.
78. High-climbing vine; achene epappose, unbeaked ..... 75. *Wulffia*
78.′ Terrestrial herbs; achene with pappus often present, a small beak sometimes present.
79. Bracts narrow, straight ..... 73. *Viguiera*
79.′ Bracts broad, curved ..... 74. *Wedelia*
10.′ Fruit not falling as a simple, dry achene, either baccate or the achene united with the involucral bracts or palea and falling as a coalesced unit (utriculate), sometimes with hooks or spines.
80. Fruit thin with broad wings (flat, compressed bracts) ..... 45. *Delilia*
80.′ Fruit plump, wingless.
81. Fruit achenelike with prominent hooks or spines (formed on the enveloping involucre); heads sessile ..... 47. *Acanthospermum*
81.′ Fruits without hooks or spines; heads pedunculate.
82. Fruit baccate or drupaceous, the fleshy or soft-leathery tissues formed by the pericarp or involucre.
83. High-climbing vines; fruits free from the subtending, conspicuous, pointed paleas; ray florets numerous, showy ..... 75. *Wulffia*
83.′ Erect, slender herbs or shrubs; fruits enclosed in a fleshy involucre; ray florets solitary or inconspicuous; paleas obscure or wanting.
84. Ray floret yellow, solitary; outer 2 involucral bracts fused and enveloping the achene and inner bracts ..... 46. *Milleria*
84.′ Ray florets white, several; outer involucral bracts separate, open apically ..... 49. *Clibadium*
82.′ Fruit dry, formed by coalescence of the achene with involucral bracts or paleas.
85. Ligules copiously pubescent beneath; disc corollas apically black-pilose;

foliaceous bracts below the heads (upper leaves) alternate ..... 67. *Sclerocarpus*

85.′ Ligules glabrate beneath; disc corollas without black hairs; leaves and bracts all opposite ..... 51. *Melampodium*

1.′ Leaves alternate or restricted to a basal rosette.

86. Leaf tips and involucre spiny ..... 100. *Cirsium*

86.′ Leaves and involucre not spiny.

87. Involucre of numerous, broad, colored, strawlike, persistent bracts; cultivated ornamental with large (more than 3 cm across) showy heads ..... 41. *Helichrysum*

87.′ Involucre not as above; heads mostly smaller.

88. Heads ligulate; florets perfect; corollas 5-denticulate, yellow or white; achenes conspicuously sulcate, often linear; pappus mostly of silky bristles; sap milky.

89. Pedicels tomentose; tawny hairs over 5 mm long conspicuous on leaves or stems; leaves mostly denticulate, not incised ..... 107. *Hieracium*

89.′ Pedicels glabrate; tawny hairs over 5 mm long lacking (gland-tipped bristles sometimes present); leaves often incised.

90. Leaves mostly cauline; pappus of both fine hairs and bristles ..... 109. *Sonchus*

90.′ Leaves in a basal rosette; pappus of bristles or fine hairs but not of both.

91. Heads less than 7 mm tall; inflorescence a many-headed, scapose panicle ..... 111. *Youngia*

91.′ Heads more than 10 mm tall; inflorescence few-(or 1-)headed.

92. Leaves glabrate; inflorescences unbranched; paleas wanting ..... 110. *Taraxacum*

92.′ Leaves copiously pubescent; inflorescences branched; paleas present ..... 108. *Hypochoeris*

88.′ Heads radiate or discoid; florets mostly bisexual; corollas variously colored; achenes sometimes ribbed but seldom sulcate, seldom linear; pappus various; sap clear.

93. Anther tips sterile but not differentiated into distinct, hyaline, ligular appendages; anthers bases tailed, always present.

94. Scapose herbs, leaves restricted to a basal rosette; heads single.

95. Heads conspicuously radiate, the rays showy; heads more than 30 mm across; cultivated plant, not fruiting in Panama ..... 102. *Gerbera*

95.′ Heads inconspicuously radiate or disciform; heads less than 20 mm across; native plants fruiting in Panama ..... 101. *Chaptalia*

94.′ Leafy stemmed herbs, shrubs or vines, the stems leafy; peduncles borne on leafy stems, mostly in inflorescences.

96. Leaves subentire or inconspicuously denticulate; heads solitary or in few-headed (less than 10) inflorescences.

97. Heads solitary, large; involucre multiseriate, more than 20 mm long; florets orange or red ..... 104. *Lycoseris*

97.′ Heads in several-headed inflorescences, smaller; involucre 1–2-seriate, less than 20 mm long; florets yellow ..... 106. *Trixis*

96.′ Leaves prominently lobed; heads in many-headed inflorescences.

98. Erect herb or shrub; leaves glabrate above and lanate beneath; involucral bracts more than 10 mm long ..... 105. *Onoseris*

98.′ Woody vine; leaves tomentose on each side; involucral bracts less than 10 mm long ..... 103. *Jungia*

93.′ Anther tips sterile and differentiated into ligulate, hyaline appendages; anther bases mostly obtuse, rarely wanting.

99. Heads radiate, disciform, or unisexual; florets of at least 2 kinds.

100. Involucral bracts with distinct, brownish or yellowish, sometimes hyaline borders.

101. Leaves less than 12 mm wide; heads less than 15 mm across; creeping native plants ..... 78. *Chrysanthellum*

101.′ Leaves more than 12 mm wide; heads more than 25 mm across; erect cultivated plants ..... 93. *Chrysanthemum*

100.′ Involucral bracts sometimes scarious-margined but without distinct borders.

102. Leaves compound, deeply divided or strongly 3-nerved from near the base.

103. Heads unisexual, the two sexes in different-appearing heads (non-functional parts present but much reduced).
104. Leaves deeply dissected, the segments narrow; staminate and pistillate heads on the same plant ..... 54. *Ambrosia*
104.′ Leaves not dissected; staminate and pistillate heads on different plants (dioecious).
105. Heads discoid; involucre less than 10 mm tall ..... 35. *Baccharis*
105.′ Heads disciform or radiate, the outer florets often few and inconspicuous; involucre more than 15 mm tall ..... 104. *Lycoseris*
103.′ Heads perfect, both sexes present and functional in each head.
106. Involucre of valvate, weakly connate bracts, sometimes with an outer series of short, free bracts; pappus of numerous silky bristles.
107. Leaves entire; florets yellowish or whitish; woody vine ..... 99. *Senecio*
107.′ Leaves toothed or lobed; florets pinkish or whitish; herb ..... 95. *Erechtites*
106.′ Involucre of several-seriate, overlapping, free bracts; pappus of awns, scales, or wanting, not of bristles.
108. Involucre more than 20 mm across; peduncles elongate, conspicuously thickened and fistulose apically ..... 71. *Tithonia*
108.′ Involucre smaller; peduncles not conspicuously thickened apically or fistulose.
109. Inflorescence well-defined, composed of 10–800 heads; heads, exclusive of rays, less than 8 mm tall.
110. Leaves dissected; herbs to 1 m tall.
110a. Ligules 5, less than 1 mm long, inconspicuous; outer involucre of 5 ovate bracts ..... 55. *Parthenium*
110a.′ Ligules 8 or more, more than 2 mm long; involucre of numerous lanceolate bracts ..... 93. *Chrysanthemum*
110.′ Leaves serrate or subentire, unlobed; shrubs or trees mostly over 1 m tall ..... 49. *Clibadium*
109.′ Inflorescence ill-defined, composed of a few aggregated heads; heads more than 10 mm tall.
111. Disc florets with black hairs near the apex; involucral bracts in 2 unlike series, the outer foliaceous, the inner shorter ..... 67. *Sclerocarpus*
111.′ Disc florets without black hairs; involucral bracts numerous in several graded series.
112. Achene apically depressed between the awns; pappus of two stout, basally flattened, strigose awns ..... 69. *Simsia*
112.′ Achene apically round or flat; pappus of awns and scales, of scales, or wanting, not of awns alone ..... 73. *Viguiera*

102.′ Leaves simple, toothed or lobed, the sinuses not extending halfway to the midvein, mostly not 3-nerved from near the base, mostly pinnately veined with a single midvein or digitate with more than 3 veins.
113. Pappus of silky or strigose bristles.
114. Heads large, the involucre more than 3 cm across; achene and pappus bristles together more than 20 mm long ..... 104. *Lycoseris*
114.′ Heads smaller; achene shorter.
115. Heads radiate, the peripheral florets pistillate and the ligules manifestly exceeding the style branches, pappus and disc florets.
116. Leaves reduced to scales or spines; midvein of involucral bracts slightly enlarged apically ..... 34. *Aster*
116.′ Plants with normal, broad leaves, not spiny; midvein of involucral bracts not enlarged apically.
117. Achenes compressed; herbs; ray florets white, bluish, or purplish ..... 37. *Erigeron*

117.′ Achenes terete; mostly shrubs or trees; all florets yellow or orange ..... 99. *Senecio*

115.′ Heads disciform, the peripheral florets perfect (*Archibaccharis*) or the ligules not exceeding the style branches, pappus, and disc florets.

118. Achene compressed 2(3)-ribbed; anthers tailless.

119. Herbs; plants perfect, both staminate and pistillate florets functional in each head ..... 36. *Conyza*

119.′ Shrubs or vines; plants dioecious, one sex not functional on each plant ..... 33. *Archibaccharis*

118.′ Achene plump, sometimes 5-ribbed; anthers mostly tailed.

120. Leaves scabrous above; receptacles paleaceous; verrucose hairs present ..... 97. *Neurolaena*

120.′ Leaves soft or smooth on both sides; receptacles naked; hairs not of verrucose type.

121. Involucre of an inner series of narrow, similar bracts more than 6 mm long and an outer (calyculate) series of minute, similar bracts.

122. Leaves entire; florets yellowish or whitish; woody vine ..... 99. *Senecio*

122.′ Leaves toothed or lobed; florets pinkish or whitish; herb ..... 95. *Erechtites*

121.′ Involucre of graded bracts in several series, the innermost mostly 6 mm long, often broad.

123. Stems conspicuously winged; achene (with pappus) more than 6 mm long ..... 43. *Pterocaulon*

123.′ Stems wingless or obscurely so; achene (with pappus) less than 6 mm long.

124. Involucral bracts narrow, acicular; leaves, including petiolar region, saliently dentate ..... 39. *Blumea*

124.′ Involucral bracts obtuse; leaves entire or serrate, entire in the petiolar region.

125. Heads glomerate, the pedicels obscure or wanting; leaves less than 10 mm wide, wooly beneath ..... 40. *Gnaphalium*

125.′ Heads with evident pedicels; leaves more than 10 mm wide, puberulent or glabrate beneath.

126. Leaves with stalked glands beneath; nectary of the staminate disc florets small ..... 42. *Pluchea*

126.′ Leaves sometimes glandular-punctate but without stalked glands; nectary of the solitary staminate disc floret much larger than the ovary ..... 44. *Tessaria*

113.′ Pappus of awns, glands, scales, or wanting.

127. Pappus present, of awns or scales.

128. Achene prominently winged ..... 72. *Verbesina*

128.′ Achene not or only indistinctly winged.

129. Shrubs; inflorescence well-defined and many-headed (10–800 heads) ..... 49. *Clibadium*

129.′ Herbs; inflorescence an ill-defined aggregate of solitary heads ..... 61. *Lasianthaea*

127.′ Pappus wanting or rudimentary, not of scales or awns.

130. Plants scapose or creeping; leaves basally narrowed or sessile; receptacle flat or convex.

131. Ray florets yellow; outer involucral bracts with whitish or yellowish margins; achene apex glandular .. 78. *Chrysanthellum*

131.′ Ray florets not yellow; outer involucral bracts without whitish margins; achene with a glandular apical peg ..... 38. *Lagenifera*

130.′ Plants erect; leaves petiolate, basally obtuse or truncate; receptacle hemispherical ..... 93. *Chrysanthemum*

99.′ Heads discoid; florets all alike, all tubular, all perfect; corolla equally 4–5-lobed or with 1 deep sinus and thus zygomorphic.
132. Involucre cylindrical of numerous, valvate, slightly connate bracts in one series; leaves often saliently toothed; pappus of fine, weak, white, silky bristles ..... 94. *Emilia*
132.′ Involucre mostly campanulate to funnelform of overlapping, marginally free bracts in several graded series; leaves serrate to entire; pappus various but not as above.
133. Paleas present; achenes mostly compressed (not in *Neurolaena*).
134. Leaves 3-nerved from near the base; herbs.
135. Leaves eglandular; pappus of minute scales ..... 60. *Garcilassa*
135.′ Leaves glandular beneath; pappus of strigose awns ..... 59. *Eleutheranthera*
134.′ Leaves 1-nerved; shrubs or vines.
136. Achenes prominently winged ..... 72. *Verbesina*
136.′ Achenes unwinged.
137. Leaves glabrous above; herbs less than 80 cm tall; heads sessile, solitary, or paired on a leafy rhachis; pappus of stout awns ..... 83. *Trichospira*
137.′ Leaves pubescent above; herbs or shrubs over 80 cm tall; heads in open, pedunculate, many-sided inflorescences; pappus of strigulose bristles.
138. Leaves with numerous, minute glands beneath; heads bisexual; verrucose hairs present ..... 97. *Neurolaena*
138.′ Leaves eglandular; heads functionally unisexual; verrucose hairs wanting ..... 33. *Archibaccharis*
133.′ Paleas wanting; achenes various.
139. Heads united into glomerules in a common involucre of indurate bracts, this sometimes subtended by foliaceous bracts as well, the glomerules mostly appearing as sessile fascicles; herbs.
140. Leaves mostly basal on the lower one half of the stem, the lower surfaces with long, stout hairs; glomerules on mostly leafless peduncles with outer bracts (leaves) appressed to the glomerules, glomerules wanting on upper leaves.
141. Glomerules sessile on an elongate spike; glomerules narrow, ellipsoidal ..... 7. *Pseudelephantopus*
141.′ Glomerules mostly terminal, a few sessile ones present; glomerules as broad as tall, globose, or campanulate ..... 6. *Elephantopus*
140.′ Leaves mostly cauline, the lower surfaces whitish-lanate beneath the long hairs; glomerules mostly on leafy stems, the outer bracts (leaves) foliaceous, not appressed to the glomerule.
142. Involucral bracts glabrous or with a few long hairs; heads narrow, ellipsoidal ..... 8. *Rolandra*
142.′ Involucral bracts pilose; heads oblong ..... 9. *Spiracantha*
139.′ Heads all distinct, not in a common involucre, if appearing in a sessile fascicle, the heads distinct; herbs, vines, or shrubs.
143. Heads on elongate peduncles, subtended by serrate subinvolucral bracts resembling the leaves (glandular-punctate) ..... 1. *Centratherum*
143.′ Heads sessile or nearly so, bracts, when present, subentire.
144. Heads in sessile glomerules on leafy or leafless branches.
145. Leaves narrow, chartaceous, basally narrowed; herbs; pappus of low, connate scales ..... 4. *Struchium*
145.′ Leaves broad, coriaceous, basally rounded; woody vines; pappus of strigose bristles (awns) ..... 2. *Piptocarpha*
144.′ Heads individually sessile or pedicellate but not in sessile glomerules.
146. Achenes with a few, flat, elongate, awnlike, twisted, strap-like bristles; head with few (to 6) florets ..... 3. *Pollalesta*

146.′ Achenes with many strigose bristles and sometimes short hairs or scales; heads mostly with many florets.
147. Leaves often with pointed lobes; style branches glabrate, lacking conspicuous hairs; achenes glabrate towards the base, eglandular.
148. Involucral bracts drying with prominent, contrasting veins, eglandular; leaves 1-nerved ..... 97. *Neurolaena*
148.′ Involucral bracts with obscure venation, minutely glandular; leaves 3–5-nerved from a point well above the base ..... 20. *Decachaeta*
147.′ Leaves unlobed or the lobes rounded; style branches pilose; achenes pilose or hispid, sometimes glandular ..... 5. *Vernonia*

I. VERNONIEAE

Vernonieae Cass., Jour. Phys. 88: 203. 1819. TYPE: *Vernonia* Schreb.

Vernoniaceae Bessey, Ann. Missouri Bot. Gard. 2: 163. 1915. TYPE: *Vernonia* Schreb.

Perennial *herbs* or *shrubs*, rarely *trees*, pubescence often of 1-celled, elongate hairs. *Leaves* mostly alternate, sometimes in a basal rosette, entire, subentire, or sometimes dentate or dissected, sessile or petiolate. *Inflorescences* various, in one subtribe the heads separate, in the other subtribe the heads united in glomerules with a common receptacle, these sometimes arranged in spikes or racemes. *Heads* discoid, florets mostly all perfect, all fertile, mostly all alike and tubular, but the outer florets differentiated in some genera; involucral bracts in evenly graded overlapping series; receptacle mostly flat, naked; corollas white, pink, purplish, rarely blue, never yellow, mostly tubular, equally 3–5-dentate but sometimes with one deeper suture; anthers appendaged, basally obtuse or auriculate (caudate-sagittate in *Piptocarpha*); style branches slender, elongate, uniformly pubescent, inconspicuously stigmatic near the base of the ventral surfaces: *Achenes* often ribbed, mostly terete or nearly so; pappus mostly of strigose bristles, sometimes of scales or coroniform.

This tribe may be recognized by its usually alternate leaves, its involucre of similar imbricate bracts in graded series, and its slender, pubescent style branches. It includes two subtribes which differ markedly in the appearance of the inflorescences; the Vernoniinae having open, distinct, and usually pedicellate heads, and the Elephantopodinae having the heads united into glomerules which are tightly enveloped by subinvolucral bracts. The tribe is best represented in the New World but there are numerous species of *Vernonia* in Africa. Augier & Du Merac (1951) argued that the Vernonieae is a primitive tribe stemming from tropical South America.

a. Heads separate from each other; heads often with many florets (Vernoniinae).
b. Pappus a ring (corona) shorter than the achene; achene glabrous, copiously glandular ..... 4. *Struchium*
bb. Pappus of strigose bristles or of scales longer than the achene; achene eglandular or sparingly glandular, sometimes pubescent.
c. Inner involucral bracts awn-tipped; outer involucral bracts leaf-like, widely spreading; pappus easily deciduous ..... 1. *Centratherum*

cc. Involucral bracts awnless, indurate, and scalelike, mostly appressed to the head; pappus persistent.
d. Heads with 1–6 florets; leaves tomentose beneath with stellate or dendritic hairs.
e. Leaves coriaceous, concolorous; involucre broad, the bracts apically puberulent with arachnoid hairs ..... 2. *Piptocarpha*
ee. Leaves chartaceous, discolorous; involucre narrowly tubular, the surface of the bracts apically glabrous but ciliate with long, transparent hairs ..... 3. *Pollalesta*
dd. Heads with more than 6 florets; leaves glabrate or pubescent beneath, mostly with simple hairs ..... 5. *Vernonia*
aa. Heads in glomerules and united into a common receptacle; heads with few (1–5) florets (Elephantopodinae).
f. Leaves distinctly petiolate, conspicuously white-tomentose beneath, distributed throughout the stem; heads with 1 floret; corollas 4-lobed; pappus of scales.
g. Glomerules sessile, globose, ebracteate; achene glandular, yellowish; pappus a continuous crown to 0.3 mm high ..... 8. *Rolandra*
gg. Glomerules usually pedunculate, capitate, bracteate; achene eglandular, grayish; pappus of 10 deciduous scales at least 0.5 mm long ..... 9. *Spiracantha*
ff. Leaves obscurely petiolate, not conspicuously white-tomentose, reduced or absent above; heads with 4 florets; corollas 5-cleft; pappus of bristles.
h. Glomerules broad, several bracteate, many-headed; involucral bracts in 2 series, membranous throughout; pappus of straight bristles ..... 6. *Elephantopus*
hh. Glomerules narrow, ebracteate, several-headed; involucral bracts in 4 series, green at tip, hyaline at base, on nerve, and margins; pappus of bristles, at least two of which are spirally twisted or doubly bent ..... 7. *Pseudelephantopus*

A. VERNONIINAE

THOMAS S. ELIAS[4,5]

Vernoniinae Less., Linnaea 5: 136. 1830. "Vernonieae." TYPE: *Vernonia* Schreb.

1. CENTRATHERUM

Centratherum Cass., Bull. Soc. Philom. 1817: 31. 1817. TYPE: *C. punctatum* Cass.

Ampherephis H.B.K., Nov. Gen. Sp. Pl. 4: 31. 1818.
Sphixia Schrank, Pl. Rar. Hort. Monac. *tab. 80.* 1819.
Amphibecis Schrank, Syll. Ratisb. 1: 86. 1824.
Crantzia Vell., Fl. Flum. Ic. 8, *tab. 153.* 1827 (1835).
Decaneurum DC., Arch. Bot. (Paris) 2: 516. 1833.
Phyllocephalum Blume, Bijdragen. 888. 1826.
Rolfinkia Zenk., Pl. Ind. 13, *tab. 14.* 1837.
Wightia Spreng. ex. DC., Prod. 5: 67. 1836.

Herbs to *subshrubs*, often diffusely branched; branches terete, glabrescent to villous. *Leaves* alternate, petiolate; blades lanceolate, ovate, elliptic or obovate, acute to subacuminate at the apex, cuneate at the base, marginally serrate, rarely entire, pubescent. *Inflorescences* axillary to terminal; involucre broadly hemispherical to broadly campanulate. *Heads* discoid with many florets; involucral

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[5] Based in part on a preliminary manuscript prepared in 1963 by James A. Duke, Plant Taxonomy Laboratory, United States Department of Agriculture, Agricultural Research Service, Beltsville, Maryland 20705. This contribution by Dr. Duke is gratefully acknowledged.

bracts in several series, the outer bracts foliaceous, the inner bracts erect, appressed, membranous to scarious; receptacle flat to subconvex, naked; florets regular, corolla narrowly tubular, 5-lobed, purplish to bluish; stamens 5, the anthers sagittate, obtuse at the base, exserted; ovary oblong, compressed, style slender, the branches exserted. *Achenes* 8–10-costate, oblong to cylindric; pappus of few to many bristles, the bristles short, caducous.

Centratherum is a small pantropical genus of about eight species with only one reported in Panama.

1. **Centratherum punctatum** Cass., Dict. Sci. Nat. 7: 384. 1817.—FIG. 2.

Apherephis aristata H.B.K., Nov. Gen. Sp. Pl. 4: 32, *tab. 314.* 1818.
Baccharoides punctatum Kuntze, Rev. Gen. Pl. 320. 1891.

Herbs or low *subshrubs* to 5 dm tall, upright, sometimes from runners, single-stemmed or many-branched, lignescent; branches terete, ascending, often striate, villous to tomentose. *Leaves* lanceolate to ovate to obovate, acute at the apex, cuneate at the base, marginally entire to pauciserrate (4–6 pairs of teeth), 1.5–5(–6) cm long, 0.5–4 cm broad, glandular punctate and villosulous on both surfaces, lateral veins ascending, 3–6 pairs, inconspicuous. *Inflorescences* sessile, solitary, terminating the branches. *Heads* discoid with many florets; involucre broadly hemispherical, the outer involucral bracts 6–15, foliaceous, curved and spreading, the inner involucral bracts scariose, 4–6-seriate, narrowly deltoid, apically acute to obtuse, spinescent, the awns 1–4 mm long, awns and involucral bracts ciliolate; receptacle flat, alveolate, naked; corolla tube narrowly cylindric, expanding slightly at the apex, purple, 5–7 mm long, 5-lobed, the lobes linear to lanceolate, 1–2 mm long; stamens 5, the anthers 1–1.5 mm long, apically acute, obtusely sagittate at base; styles 6–7 mm long, bilobed, the lobes puberulous, 1–2 mm long, acute. *Achenes* narrowly turbinate, weakly ribbed, 1–2 mm long, ultimately epappose; pappus of deciduous filiform scales 1–2 mm long, antrorsely puberulent.

Locally common in rocky or gravelly savanna-like areas, this species can be found near sea level but occurs more frequently from 600–1200 m altitude. This species appears to be very close to *Centratherum intermedium* of Brazil. In fact, the distinction between the two species is less than satisfactory.

CANAL ZONE: Ancón Hill, *Greenman & Greenman 5120* (MO). CHIRIQUÍ: Between Boquete and David, *Ebinger 743* (MO). Boquete, Llanos Francia, 4 mi from Boquete toward Dolega, *Dwyer & Hayden 7582* (GH, MO). Llanos Francia, *Dwyer & Lallathin 8710* (MO). Frances Arriba School, ca. 14 mi N of David, *Lewis et al. 653* (GH, MO, NY, US). 5 mi S of Boquete, *McDaniel 6799* (MO); *Allen 4690* (MO). 8 km N of David, *Partch 69–145* (MO). Boquete, *Stern et al. 1218* (MO). Vic. of Boquete, *Woodson & Schery 790* (MO). COCLÉ: S of El Valle, *Allen 2857* (MO). Río Hato airstrip, *Burch et al. 1137* (GH, MO, NY, US); *Tyson & Blum 2557* (MO). Between Las Margaritas and El Valle, *Woodson et al. 1262, 1772* (both MO, NY). HERRERA: 10 mi S of Ocú, *Tyson et al. 2873* (MO). PANAMÁ: Hills near Campana, *Allen 1307* (MO, NY). Vic. of Pacora, *Allen 1115* (MO). Camino de Burunga, Nuevo Emperador, *Austin*

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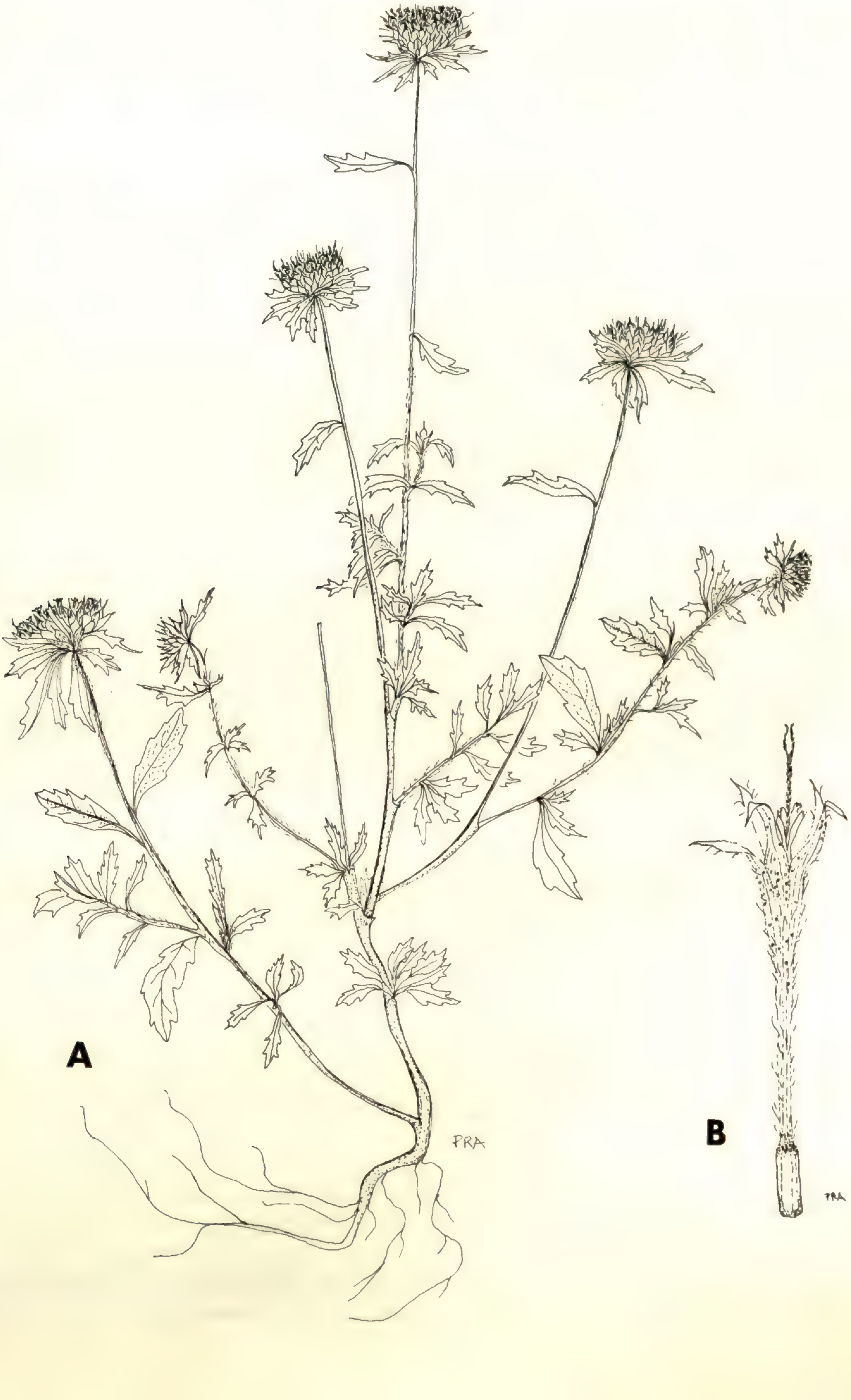
FIGURE 2. *Centrantherum punctatum* Cass.—A. Habit (× 3/5). [After *Dwyer 8710* (MO).] —B. Floret (× 8½). [After *Luteyn 1478* (MO).]


A
B
PRA
PRA

23 (MO). Road between Goofy Lake in Cerro Azul and main hwy., *Correa & Dressler 431* (MO). Savanna near Río Pacora and Chepo Hwy., *Duke 5905* (MO). Road toward top of Cerro Campana, *Duke 5917* (MO). Road from Pan-Am Hwy. to Coronado Beach, *Duke 11794* (MO). Cerro Campana, *Ebinger 923* (MO). Río Tocumen, *Hunter & Allen 242* (MO, NY). SE slope of Cerro Campana, *Lewis et al. 3122* (MO, NY). Nuevo Emperador, *Peralta 27* (MO). Sabana de Tortuga, *Pittier 3339* (NY). Penonomé and vic., *Williams 90* (NY). Near Arraiján, *Woodson et al. 1397* (MO, NY).

2. PIPTOCARPHA

Piptocarpha R. Brown, Trans. Linn. Soc. London 12: 121. 1817 (1818). TYPE: *P. brasiliana* Cass.

Carphobolus Schott, Spreng. Syst. 4: Cur. Post. 409. 1827.
Monanthemum Griseb., Fl. Brit. W. Ind. 354. 1861.

Shrubs, frequently scandent or climbing; branches pubescent with stellate or lepidote trichomes. *Leaves* alternate, petiolate; blades large, ovate to lanceolate, entire to subentire, pinnately veined, glabrous above, often tomentose beneath. *Inflorescences* usually aggregated in axillary corymbs, umbels or sessile clusters, or in terminal panicles. *Heads* with 3–20 florets; involucre campanulate, cylindrical-campanulate to turbinate, involucral bracts imbricate in few to several series, the outer bracts smaller, obtuse, the inner bracts often caducous with the achenes; receptacle convex, naked; florets regular, narrow tubular, 5-lobed; stamens 5, sagittate, the auricles subcaudate, style slender, stigma bifid, the branches usually pubescent. *Achenes* 10-costate, glabrous or rarely pilose, truncate; pappus of bristles in two series, the inner series filiform, long, equal, the outer series linear, shorter, unequal or occasionally lacking.

This small neotropical genus is centered in Brazil, extending northward into the West Indies and Central America. A single species is reported from Panama.

1. **Piptocarpha chontalensis** Baker in Mart., Fl. Bras. 6(2): 132. 1873. TYPE: Nicaragua, *Tate 162* (not seen).—FIG. 3.

P. costaricensis Klatt, Bull. Soc. Roy. Bot. Belgique 31(1): 184. 1892.

Shrubs to 20 m tall, scandent; branches terete or striate, cinereous-tomentose. *Leaves* petiolate; petioles sulcate, 5–20 mm long; blades oblong to broadly ovate, acute to short-acuminate at the apex, obliquely rounded to subcordate at the base, marginally entire to sparsely denticulate, 6–18 cm long, 4–10 cm broad, plane, lustrous and glabrous above, with short-stalked, stellate, cinereous trichomes beneath, lateral veins ascending, 6–8 pairs. *Inflorescences* axillary, in dense pedunculate corymbs subtended by reduced leaves; heads subsessile in few-headed glomerules. *Heads* discoid with 6 florets, involucre ovoid, involucral bracts 4–7-seriate, subequitant, the bracts usually less than 15, ovate to deltoid, acute to obtuse at the apex, often glandular, the inner often coiling and falling with the achene; corolla salverform, white, 6–8 mm long, 5-lobed, the lobes linear-deltoid, 1.5–3 mm long, recoiled; stamens 5, the anthers 2–3 mm long, apically acute, basally caudate-sagittate; styles 6–7 mm long, the branches 1.5–2.5 mm long, apically acute, antrorsely puberulent. *Achenes* 2.5–3.2 mm long, 10-costate, glabrous or glandular; pappus white, biseriate, the inner bristles 5.5–7 mm long, the outer series much shorter, unequal, usually less than 1 mm long.

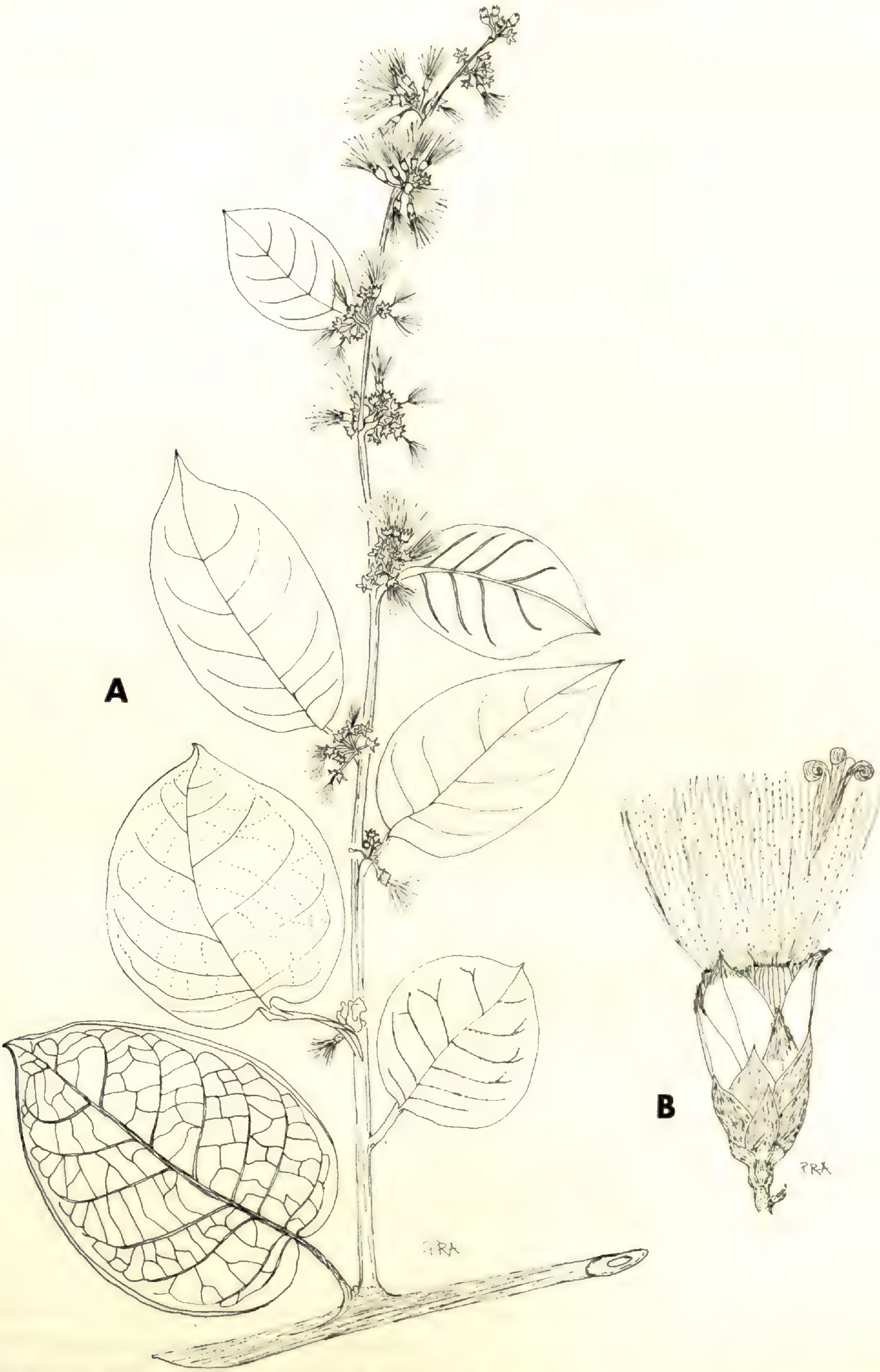


FIGURE 3. *Piptocarpha chontalensis* Baker.—A. Flowering branch (× 3/5). [After *Skutch 4270*, Costa Rica (MO).]—B. Head (× 4½). [After *Molina & Molina 25646*, Honduras (MO).]

Primarily a lowland species, *Piptocarpha chontalensis* can often be recognized in the field by its large leaves, scandent or climbing habit, and white heads. This species extends into Costa Rica and Nicaragua.

COCLÉ: Vic. of La Mesa, N of El Valle de Antón, 1000 m, *Allen 2372* (NY, MO). DARIÉN: Headwaters of Río Chico, 170–250 m, *Allen 4628* (MO). Manené to mouth of Río Cuasí, *Kirkbride & Bristan 1390* (MO, NY). Caña, 335 m, *Williams 720* (NY). PANAMÁ: Cerro Jefe, *Duke 9447* (MO).

3. POLLALESTA

Pollalesta H.B.K., Nov. Gen. Sp. Pl. 4: 46. 1820. TYPE: *P. vernonioides* H.B.K.

Oliganthes Cass., Bull. Sci. Soc. Philom. Paris. 10. 1817.
Odontoloma H.B.K., Nov. Gen. Sp. Pl. 43. 1820.
Dialesta H.B.K., Nov. Gen. Sp. Pl. 4: 45. 1820.
Adenocyclus Less., Linnaea 4: 337. 1829.

Shrubs or small *trees*, usually diffusely branched; branches terete, often tomentose. *Leaves* alternate, petiolate; blades often large, lanceolate to elliptic, usually cuneate at the base, acute to acuminate at the apex, entire, glabrate to densely tomentose. *Inflorescences* terminal, usually aggregated in dense corymbiform panicles. *Heads* with 1–6 florets; involucre cylindric to narrowly campanulate, involucral bracts few, imbricate in several series, multiseriate, membranous to scarious; receptacle subconvex, naked; corolla tubular, 5-lobed; stamens 5, the anthers basally sagittate; style slender, bilobed. *Achenes* truncate, 8–10-costate; pappus variable, often caducous, often in two series, the outer series small, more or less united into a cup, the inner series of 0–15 linear, aristate, bristles.

Pollalesta is a small genus confined to the New World and ranges from Costa Rica and Panama to Colombia, Venezuela, Ecuador, Peru and northern Brazil. A single species is reported from Panama.

Literature:

Aristeguieta, L. 1963. El género *Oliganthes* de Madagascar y su equivalente americano *Pollalesta*. Bol. Soc. Venez. Ci. Nat. 23(103): 255–288.

1. **Pollalesta discolor** (H.B.K.) Aristeguieta, Bol. Soc. Venez. Ci. Nat. 23(103): 275. 1963.—FIG. 4.

Dialesta discolor H.B.K., Nov. Gen. Sp. Pl. 4: 45. 1820. TYPE: Colombia, *Humboldt & Bonpland s.n.* (not seen).
Oliganthes discolor (H.B.K.) Schultz-Bip., Linnaea 20: 502. 1847.

Large *shrub* to small *tree*; branchlets subterete, often obscured by the densely scurfy indument. *Leaves* petiolate; petioles 5–25 mm long; blades elliptic to ovate, acute to acuminate at the apex, rounded to obliquely attenuate at the base, marginally entire, 6–18 cm long, 3.5–6 cm broad, plane and glabrous to strigillose above, lanulose and resinous beneath, lateral veins ascending, 5–12 pairs, immersed above, prominulous beneath. *Inflorescences* shortly pedunculate in dense corymbs, these aggregated in irregular corymbiform panicles. *Heads* with 2 florets; involucre cylindric to narrowly campanulate, the involucral bracts fewer than 10, equitant, imbricate, 4–6 mm long, the outer bracts squamiform, lanulose, the

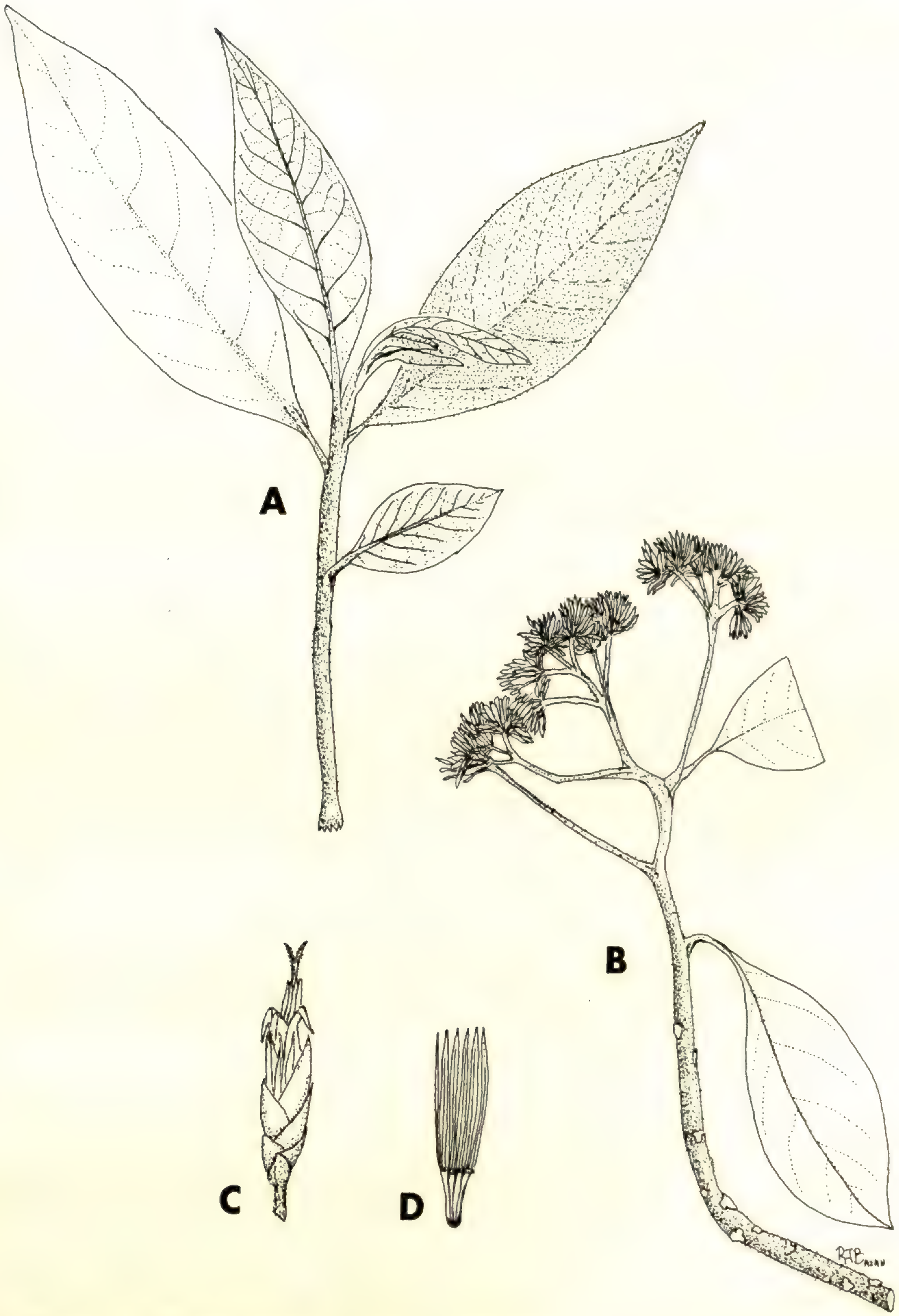


FIGURE 4. *Pollalesta discolor* (H.B.K.) Aristeguieta.—A. Leafy branch (× 7/10).—B. Flowering branch (× 7/10).—C. Head (× 3⅓).—D. Achene (× 3⅓). [After *Tyson* 6433 (MO).]

inner bracts obovate, scarious, often with a green mid-portion or purple tip, 4–5 mm long; corolla tubes cylindric, white, 4–5 mm long, 5-lobed, the lobes linear-deltoid, 1.5–2.5 mm long; stamens 5, the anthers 2 mm long, apically acute, acutely sagittate at base; styles 5–6.5 mm long, bilobed, the branches 1–2 mm long, apically acute, antrorsely puberulent. *Achenes* narrowly turbinate, 1.8–2.2 mm long, 8–10-costate, very sparsely puberulent; pappus biseriate, the inner series of 5–8 narrowly oblong bristles 3–3.5 mm long, apically lacerate, the outer series of 5–10 bristles, 0.2–0.4 mm long.

Pollalesta discolor occurs from Costa Rica to Colombia and Venezuela. The trees, with white heads, often reach 13 m in height.

CHIRIQUÍ: Jaramillo, Boquete, 4500 ft, *Davidson 1276* (MO). PANAMÁ: 3 mi from Interam. Hwy. on Cerro Campana dirt road, *Correa & Dressler 392* (MO). Road to Cerro Campana, 2000 ft, *Tyson 6433* (MO). VERAGUAS: Hills W of Sona, *Allen 1036* (MO).

4. STRUCHIUM

Struchium P. Browne, Civ. Nat. Hist. Jam. 312, *tab. 34, fig. 2.* 1756. TYPE: *S. herbaceum* St.-Hilaire.

Athenaea Adanson, Fam. 2: 121. 1763, not Sendtn. (Solanaceae), nom. cons.
Sparganophorus (Vaillant) Crantz, Inst. Rei Herb. 1: 261. 1766.

Annual *herbs*, single-stemmed or sparingly branched; branches erect. *Leaves* alternate, simple, petiolate, subentire to variously dentate, pinnately veined. *Inflorescences* single or glomerate, whitish to purplish. *Heads* discoid; involucre hemispheric, the involucral bracts numerous, imbricate in several series, marginally scarious, acuminate to subspinescent at the apex; corolla tubular to salverform, 3–4-lobed, the lobes valvate; anthers oblong, sagittate to acute at the base; style slender, bifid, the branches hirtellous. *Achenes* angular, costate, turbinate; pappus coroniform.

A monotypic genus of lowland areas, *Struchium* ranges from Southern Mexico, the West Indies and Central America to tropical South America, and is reportedly adventive in Africa.

1. **Struchium sparganophorum** (L.) Kuntze, Rev. Gen. Pl. 366. 1891.—FIG. 5.

Ethulia sparganophora L., Sp. Pl., ed. 2. 1171. 1763.
Struchium herbaceum P. Browne ex St.-Hilaire, Expos. Fam. 1: 406. 1805.
Ethulia struchium Swartz, Prod. Veg. Ind. Occ. 3: 1297. 1806.
Sparganophorus struchium Poir. in Lam., Encycl. Meth. 7: 302. 1806.
S. fasciatus Poir. in Lam., Encycl. Meth. 7: 302. 1806.
Struchium americanum Poir. in Lam., Encycl. Meth. 7: 475. 1806.

Annual *herbs* to 1 m tall; stems puberulent to glabrous, striate. *Leaves* cauline, narrowly to broadly elliptic, denticulate, at least apically, acute to attenuate at the apex, cuneate at the base, 3–12 cm long, 1–4 cm broad, sparsely strigillose and subglandular above, more so beneath, lateral veins 7–12 pairs; petioles

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FIGURE 5. *Struchium sparganophorum* (L.) Kuntze. Plant in flower (× ⅜). [After *Wedel 2074* (MO).]

ascending, canaliculate to narrowly winged, 1–20 mm long. *Inflorescences* sessile, often glomerate in the axils. *Heads* with ca. 50 florets; involucre hemispheric, 3–5 mm long, 3–4-seriate, the bracts acuminate to subspinescent, ciliolate; corolla 1–2 mm long, purple, salverform, 3–4-lobed, the lobes ca. 0.2 mm long; stamens 3–4, the anthers oblong, 0.5–1 mm long, apically acute, basally circinate-sagittate; style 1.5–2 mm long, bifid for less than half its length, the branches acute. *Achenes* narrow, arcuately turbinate, 3–4-angled, 1.3–2 mm long, glabrous; pappus a cartilaginous corona, half as long as the achene, the corona shallowly lobed or entire.

The pappus of *Struchium sparganophorum* is unusual in the Compositae, being composed only of a fused ring or corona, devoid of bristles.

BOCAS DEL TORO: Old Bank Lagoon, *Wedel 2074* (MO). Water Valley, *Wedel 1673* (MO). CANAL ZONE: Chagres, *Fendler 142* (MO). DARIÉN: Near Refugio, 15–20 mi N of Santa Fé, *Duke 10294* (MO). Manené to mouth of Río Cuasí, *Kirkbride & Bristan 1525* (MO). Marragantí, *Williams 992* (NY). PANAMÁ: Cerro Campana, *Lewis et al. 1999* (GH, MO, US).

5. VERNONIA

Vernonia Schreb., Gen. Pl. 2: 541. 1791, nom. cons. TYPE: *V. noveboracensis* (L.) Willd.

Seneciodes Post & Kuntze, Lex. Gen. Phan. 2: 515. 1903.
Eremosis (DC.) Gleason, Bull. New York Bot. Gard. 4: 227. 1906.

Annual or perennial *herbs*, *shrubs*, or *trees*, rarely scandent, unbranched to much-branched; branches usually ascending, variously pubescent to glabrous. *Leaves* alternate, simple, usually cauline; blades various, often narrowly lanceolate to broadly ovate or elliptic. *Inflorescences* terminal or upper axillary, composed of scorpioid cymes or becoming paniculate or corymbiform or rarely reduced to solitary heads. *Heads* discoid with 1–many florets; involucre narrowly campanulate to subcylindric to broadly hemispheric, the involucral bracts in few to many series, closely to laxly imbricate, the inner series often longer, persistent and spreading at maturity; receptacle flat or subconvex; corolla regular, usually pink, purple, or white, 5-lobed; stamens 5, the anthers sagittate at the base, rounded or subacute at the apex, appendaged. *Achenes* more or less cylindric, ribbed or ribless; pappus of slender bristles or scales, biseriate, the inner series capillary, terete to slightly flattened, the outer series very short.

This large genus of perhaps 550–600 species inhabits primarily tropical regions of both the Old and New Worlds. In the New World, *Vernonia* is most abundant in South America, but extends northward through Central America into temperate North America. Six species are recognized from Panama including the naturalized Old World species, *V. cinerea*. *Vernonia scorpioides* is known from British Honduras, Honduras, Nicaragua, and tropical South America and therefore is suspected to occur in Panama.

Literature:

Gleason, H. A. 1906. A revision of the North American Vernonieae. Bull. New York Bot. Gard. 4: 144–243.

Gleason, H A. 1922. *Vernonia* and *Eremosis*. *In* North American Flora 3: 52–101.

Jones, S. B., Jr. 1973. Revision of *Vernonia* sect. *Eremosis* (Compositae) in North America. Brittonia 25: 86–115.

a. Heads with 13–36 florets.
  b. Heads pedunculate, the peduncles 5–12 mm long; inflorescences corymbose, the axes equal, strongly dichotomizing; achenes ribless; leaves with 2–4 pairs of lateral veins; bristles of the inner pappus deciduous ..... 3. *V. cinerea*
  bb. Heads sessile, subsessile, or short-pedunculate; inflorescences paniculate or corymbose, the axes unequal, sometimes monopodial; achenes ribbed; leaves with 5–20 pairs of lateral veins; bristles of the inner pappus persistent.
    c. Heads subtended by foliaceous bracts 10–15 mm long; heads with 24–36 florets; involucre 6–8 mm tall, 6–7-seriate ..... 5. *V. seemanniana*
    cc. Heads without foliaceous bracts or with only subulate bracts; heads with 18–27 florets; involucre 3–6 mm tall, 4–6-seriate.
      d. Inflorescence a sparsely or freely branched cyme; leaves broadly elliptic to broadly ovate.
        e. Leaves broadly elliptic to broadly ovate, 10–30 cm long, 5–13 cm broad, subauriculate at the base, plane and glabrous to glabrescent above; inflorescences with the individual cymes usually recurved and with 22–46 heads ..... 1. *V. brachiata*
        ee. Leaves broadly lanceolate to ovate-elliptic, 3–15 cm long, 1–5 cm broad, rounded to obtuse at the base, rugose to rarely bullate and scabrous to strigillose above; inflorescences with the individual cymes spreading and with 18 heads or fewer ..... 2. *V. canescens*
      dd. Inflorescence a much-branched corymb or panicle; leaves lanceolate ..... 4. *V. patens*
aa. Heads with 3–4 florets ..... 6. *V. triflosculosa*

1. **Vernonia brachiata** Benth. in Örst., Vidensk. Meddel. Dansk Naturhist. Foren. Kjøbenhavn 1852: 67. 1852. TYPE: Costa Rica, *Oersted s.n.* (not seen).—FIG. 6.

Cacalia brachiata (Benth.) Kuntze, Rev. Gen. Pl. 969. 1891.

Herbs or small *shrubs* to 3 m tall; branches herbaceous, striate, becoming angular, glabrous or nearly so. *Leaves* subsessile; blades broadly elliptic to broadly obovate, acute to short acuminate at the apex, subauriculate at the base, 10–30 cm long, 5–13 cm broad, marginally entire to serrulate, glabrous to glabrescent above and beneath, lateral veins ascending, 10–14 pairs. *Inflorescences* terminal, leafless, 10–30 cm high, in long, freely branched cymes, the individual cymes 10–25 cm long with 22–46 heads, straight or more often recurved, peduncles 1.4–3.8 cm long, the bracts not foliaceous, linear, to 3 mm long. *Heads* with 18–22 florets, involucre broadly campanulate, 3–4 mm high, 4–5-seriate, the involucral bracts loosely imbricate, ciliate, the outer bracts narrowly ovate to lanceolate, acute to subcuspidate, with a thickened midrib, the inner bracts oblong to oblanceolate, acute to subacute, scarious, purple-tipped; receptacle flat, alveolate, naked; corolla tubular, 4–5 mm long, 5-lobed, the lobes lanceolate; stamens 5, anthers 2–2.5 cm long, apically acute, broadly sagittate; styles 4–4.5 mm long, the 2 branches 1–2 mm long, antrorsely puberulous. *Achenes* narrowly cylindric, 2–3 mm long, faintly ribbed, puberulous; pappus biseriate, the inner bristles filiform, 4–5 mm long, persistent, the outer bristles linear, to 0.3–0.6 mm long, persistent.

A
B

Previously known in Central America only from Costa Rica, this attractive species can now be reported with certainty from western Panama. The very large leaves coupled with the long, often arching, many-headed cymes easily separate this taxon from the other Panamanian species of *Vernonia*.

BOCAS DEL TORO: Changuinola Valley, Lincoln Creek, *Dunlap 425* (NY). CHIRIQUÍ: Corotú, 6 km W of airport of Puerto Armuelles, 100–200 m, *Liesner 10* (MO). 8 mi from Paso Canoas to Cañas Gordas, *Liesner 221* (MO).

2. **Vernonia canescens** H.B.K., Nov. Gen. Sp. Pl. 4: 35, *tab. 317*. 1820.

V. bullata Benth. in Örst., Vidensk. Middel. Dansk Naturhist. Foren. Kjøbenhavn 1852: 67. 1852.
Cacalia bullata (Benth.) Kuntze, Rev. Gen. Pl. 969. 1891.
C. canescens (Benth.) Kuntze, Rev. Gen. Pl. 969. 1891.

Shrubs or coarse *herbs* to 3 m tall, erect, sparsely to many-branched; branches lignescent, striate, often densely pubescent above, glabrescent. *Leaves* short petiolate; petioles terete to canaliculate, 3–12 mm long; blades broadly lanceolate to ovate-elliptic, acute to acuminate at the apex, rounded to obtuse at the base, 4–12 cm long, 2–5 cm broad, marginally entire to remotely denticulate, often rugose to rarely bullate, scabrous to strigillose above, densely strigillose and glandular-punctate beneath, lateral veins ascending, 8–12 pairs. *Inflorescences* terminal in sparsely branched, short-pendunculate cymes, the cymes frequently arranged in large, spreading panicles or corymbs. *Heads* with 21–24 florets, sessile; involucre broadly campanulate, 4–6 mm high, 5–6-seriate, loosely imbricate, sparsely villous, the outer bracts triangular-subulate, spinose-tipped, the inner bracts lanceolate, acuminate at the apex, scarious; receptacle flat, alveolate, naked; corolla salverform, 3.5–5 mm long, 5-lobed, the lobes narrowly triangular, 2–2.5 mm long; stamens 5, anthers 2–2.2 mm long, apically acute, basally obtusely sagittate; styles 3–5.5 mm long, the 2 branches 1.5–2 mm long, antrorsely puberulous. *Achenes* narrowly turbinate, faintly ribbed, 1–2.5 mm long, antrorsely puberulent; pappus white, biseriate, the inner bristles linear, 3–5 mm long, the outer series subulate, 0.4–1.1 mm long.

This species ranges from southern Mexico southward throughout Central America to tropical South America. In Panama, *Vernonia canescens* is a common small shrub. Specimens have been collected from Chiriquí Province with bullate leaves. Bentham segregated the bullate-leafed populations into *V. bullata*; however, the presence of a continuous gradation from the rugose to the bullate condition warrants the inclusion of *V. bullata* within the specific delimitations of *V. canescens*.

CANAL ZONE: France Field, *Blum & Dwyer 2117* (MO). Within 5 mi N of Gamboa gate, *D'Arcy 6008* (MO). Albrook, *Dwyer & Robyns 81* (MO); *Dwyer 4469, 7318* (both MO). Chagres, *Fendler 160* (MO). Ancón Hill, *Greenman & Greenman 5124* (MO); *Celestine 70* (NY, US); *Williams 26* (NY). Near Miraflores, *Greenman & Greenman 5202* (MO). Between Summit and Gamboa, *Greenman & Greenman 5234* (MO). Las Cruces Trail, *Hunter & Allen 690* (MO). Madden Forest Preserve, *Lewis et al. 5364* (MO). Navy Reservation N of Gamboa,

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FIGURE 6. *Vernonia brachiata* Benth.—A. Flowering branch (× ⅜).—B. Achene (× 13). [After *Liesner 221* (MO).]

Robyns 65–44 (MO). Balboa, *Standley 29314* (MO). 1 mi N of Summit, *Tyson et al. 2769, 2774, 2779* (all MO). Curundú, *Tyson 3477* (MO). BARRO COLORADO ISLAND: *Busey 302* (MO); *Croat 7079* (MO), *7219* (MO, NY), *7259, 7480, 8264* (all MO), *8392* (MO, NY), *9398* (MO); *Shattuck 774* (MO); *Wetmore & Abbe 208* (MO), *Woodworth & Vestal 346* (MO). CHIRIQUÍ: Central Valley of Río Chiriquí Viejo, *Allen 1344* (MO, NY). NW of Boquete, Cerro Horqueta, *Dwyer et al. 522* (F, GH, MO, NY, US). Río Chiriquí Viejo Valley, near El Volcán, *White 178* (MO). COCLÉ: Penonomé, *Williams 592* (NY). COLÓN: Santa Rita, *Gómez-Pompa et al. 3215, 3294* (both MO). HERRERA: Vicinity of Ocú, *Stern et al. 1747* (MO). 10 mi S of Ocú, *Tyson et al. 2802* (MO). LOS SANTOS: Loma Prieta, *Duke 11835, 11890* (both MO). 16 mi S of Macaracas, at Quebrada Bejuco, *Tyson et al. 2915* (MO). PANAMÁ: Taboga Island, *Allen 129* (MO). Trail between Cañazas and foot of Cordillera Central headwaters of Río Cañazas, *Allen 187* (MO). Along road to Cerro Campana, *Correa & Dressler 849* (MO). Cerro Azul, *Duke 9342* (MO); *Kant 45* (MO). Cerro Jefe, *Duke 9385, 15240* (both MO). Isla del Rey, *Duke 9523* (MO). Isla Saboga, *Duke 10351* (MO). San José Island, *Erlanson 71* (NY, US). 1 mi E of Charné, *Lazor 2207* (MO). Cerro Campana, *Porter et al. 4301, 4892* (both MO). Río Piriquete, near Capira, *Saldana 13* (MO). VERAGUAS: Carretera a Santa Fé, *Cisneros 10* (MO).

3. **Vernonia cinerea** (L.) Less. Linnaea 4: 291. 1829.

Conyza cinerea L., Sp. Pl. 862. 1753.
Seneciodes cinereum (L.) Kuntze in Post & Kuntze, Lex. Gen. Phan. 515. 1904.

Herbs to 1 m tall, erect, unbranched to freely branched; branches striate, cinereous-puberulent above, glabrescent below. *Leaves* petiolate; petioles narrowly winged, 0.5–2.0 mm long; blades narrowly elliptic to deltoid, obtuse to acute at the apex, cuneate at the base, 2–5(–8) cm long, 0.5–3.0 cm broad, marginally entire to serrate, sparsely hirtellous above, glandular-punctate and hirtellous below, lateral veins ascending, 2–5 pairs. *Inflorescences* terminal, in dichotomously branched corymbs; peduncles 5–12 mm long; bracts often foliaceous, linear, to 1.5 cm long. *Heads* with 13–23 florets; involucre campanulate, the involucral bracts laxly 3–4-seriate, the outer bracts subulate, the inner bracts narrowly lanceolate, attenuate, puberulent; receptacle flat, alveolate, naked; corolla tubular, 3–4 mm long, 5-lobed, the lobes lanceolate, to 0.5 mm long; stamens 5, the anthers 0.6–0.8 mm long, apically acute, obtusely sagittate at the base; styles 3–4 mm long, with 2(3) branches to 0.5 mm long, rarely glabrous. *Achenes* subcylindric, ribless, 1.4–2.2 mm long, antrorsely puberulent; pappus biseriate, the inner bristles linear, 3–5 mm long, deciduous, the outer bristles subulate, to 0.5 mm long, persistent.

This species is readily distinguished in the field from the rest of the genus by the more delicate appearance of the inflorescences and the pedunculate heads. Found principally in disturbed areas such as clearings, road and railway margins, and in lawns, *Vernonia cinerea* is native of tropical areas of the Old World. It has become a pantropical weed through introductions into tropical America. It extends northward into Mexico and in the United States into the Florida Keys and hammocks of extreme southern Florida.

CANAL ZONE: Balboa, *D'Arcy & D'Arcy 6020* (MO); *Dwyer 2600* (MO). Atlantic side, just E of Gatun Locks, *Duke 4299b, 4302* (both MO). Fort Sherman site, U.S. Army Tropic Test Center, *Dwyer 7193* (MO). Howard Air Force Base, SE of Kobbe Beach, *Oliver & MacBryde 1876* (GH, MO, NY, US). Balboa Station, *Porterfield s.n.* (NY). Farfan Beach area, *Tyson et al. 3181* (MO). BARRO COLORADO ISLAND: *Aviles 90* (MO); *Croat 4067, 6879* (both MO); *Ebinger 131, 132* (both MO); *Netting s.n.* (MO); *Shattuck 563* (MO); *Starry 275* (MO). PANAMÁ: Bohio Soldada, *Cowell 238* (NY). Morro Island, *D'Arcy & D'Arcy 6809* (MO). Taboga Island, *Dwyer 2786* (MO).

4. **Vernonia patens** H.B.K., Nov. Gen. Sp. Pl. 4: 41. 1818.

V. lanceolaris DC., Prodr. 5: 37. 1836.
V. pacchenis Benth., Pl. Hartw. 134. 1844.
V. aschenborniana Schauer in Ness & Schauer, Linnaea 19: 714. 1847.
Cacalia lanceolaris (DC.) Kuntze, Rev. Gen. Pl. 970. 1891.
C. patens (H.B.K.) Kuntze, Rev. Gen. Pl. 970. 1891.
Vernonia salamana Gleason, Bull. Torrey Bot. Club 46: 242. 1919.

Shrub or small *tree* to 8 m tall, freely branched; branches erect, striate, lignescent, puberulous to tomentulose on the younger stems, glabrescent. *Leaves* short petiolate; petioles terete, 2–10 cm long; blades lanceolate to narrowly oblong, acute to acuminate at the apex, cuneate to obtuse at the base, 3–15 cm long, 1–3 cm broad, marginally entire to serrulate, rugose and nearly glabrous to sparsely pubescent above, puberulent to strigillose beneath, lateral veins weakly ascending, 8–20 pairs. *Inflorescences* in terminal much-branched corymbs or panicles, the cymes becoming scorpioid. *Heads* with 21–27 florets, sessile to subsessile, foliar bracts absent; involucre broadly campanulate, 4–5 mm high, 5–6-seriate, closely imbricate, oblong to suborbicular, obtuse to apiculate at the apex, glabrous to puberulent, ciliate, pale green with brown midrib or tip; corolla salverform, 5–6 mm long, 5-lobed, the lobes triangular, 1.5–2.5 mm long; stamens 5, the anthers 1.8–2.3 mm long, apically acute, basally obtusely sagittate; styles 5–6 mm long, the 2 branches 1.5–2.5 mm long, antrorsely puberulent. *Achenes* narrowly turbinate to subcylindric, obscurely ribbed, 1.3–1.8 mm long, minutely puberulent; pappus fulvous, biseriate, the inner bristles linear, 4.0–5.5 mm long, the outer series subulate, 0.3–0.8 mm long.

This species is relatively common, extending from southern Mexico to tropical South America. Generally found near sea level, *Vernonia patens* also occurs up to approximately 1500 m elevation in thickets and disturbed areas.

BOCAS DEL TORO: Region of Almirante, *Cooper 530* (NY). CANAL ZONE: Miraflores Annex, *Blum 2175* (MO). Monkey Hill and vic., *Cowell 12, 16* (both NY). Gaillard Highway, 1 mi NW of Summit Gardens, *Croat 8884* (MO). Chagres, Isthmus of Panama, *Fendler 150* (MO). Culebra Cut, *Hunter & Allen 782* (MO, NY). Hills between Río Grande and Pedro Vidal, *Pittier 2701* (NY, US). Across railroad tracks from Summit Garden, *Tyson 6396* (MO). Ancón Hill, *Williams 18* (NY). BARRO COLORADO ISLAND: *Croat 4562, 7229, 7472, 8248, 8367, 8665, 8778, 14089* (all MO); *D'Arcy 3987* (MO, NY); *Ebinger 95* (MO); *Gentry 447* (MO). CHIRIQUÍ: Burica Peninsula, San Bartolomé, *Busey 531* (MO). Palo Santo, 3 mi N of Volcán, *Croat 13550* (MO, NY). Las Lagunas, 2 mi SW of El Volcán, *Tyson 855* (MO). COCLÉ: Penonomé, *Williams 69* (NY). COLÓN: Santa Rita, *Gómez-Pompa et al. 3004, 3211* (both MO). Río Piedras, *Stern et al. 722* (MO). DARIÉN: Vic. of Pinogana, *Allen 4307* (MO). Marragantí, *Wilson 642* (NY). HERRERA: Between Ocú and Chitré, *D'Arcy & Croat 4140* (MO, NY). Vic. of Ocú, *Stern et al. 1681, 1727* (both MO). PANAMÁ: Vic. of Arraiján, *Allen 1629* (MO, NY). Vic. of Santa Fé near Río Santa María, *Allen 4425* (MO). Isla Chepillo, *Duke 10319* (MO). Isla Espirita Santo, *Duke 10449* (MO). Río Pacora just below confluence with Río Corso, *Duke 11990* (MO). Cerro Jefe, near Río Indio, *Duke 15241* (MO). Cerro Jefe, *Dwyer et al. 7266* (MO). Cerro Campana, *Porter et al. 4321* (MO, UC). Cerro Azul, *Slater & Harrington 1* (MO). E slope of Cerro Jefe, *Tyson 3714* (MO). VERAGUAS: Vic. of Santa Fé near Río Santa María, *Allen 4425* (MO). Cañazas, *Tyson 3636* (MO).

5. **Vernonia seemanniana** Steetz in Seem., Bot. Voy. Herald 139. 1854. TYPE: Panama, *Seeman s.n.* (not seen).

Cacalia seemanniana (Steetz) Kuntze, Rev. Gen. Pl. 971. 1891.

Shrubs to 3 m tall, scandent, becoming woody at the base; branches terete, densely tomentose. *Leaves* petiolate; petioles terete, 4–10 mm long; blades ovate-lanceolate to elliptic, acute to short-acuminate at the apex, rounded at the base, 5–12 cm long, 2–5 cm broad, entire, subcoriaceous, glabrous above except for the puberulent young leaves, strigose below, occasionally resinous, lateral veins ascending, 6–12 pairs, prominently reticulate. *Inflorescences* terminal, in spreading dichasial cymes, the secondary branches strongly monopodial. *Heads* with 24–36 florets, subsessile, bracts foliaceous, 5–20 mm long, 2–5 mm broad, narrowly elliptic; the involucre broadly campanulate, 6–8 mm tall, 6–7-seriate, the involucral bracts ciliate, pubescent, the outer bracts minute, deltoid, acute, the inner bracts lanceolate to oblong, obtuse to acute, recurved; receptacle flat, alveolate, naked; corolla tubular, 4 mm long, 5-lobed, the lobes narrowly lanceolate; stamens 5, the anthers ca. 2.5 mm long, apically acute, basally acutely sagittate; styles 4–5 mm long, 2–3-lobed, the branches to 2 mm long, hispidulous. *Achenes* broadly cylindric, ribbed, 1–2 mm long, antrorsely hispidulous; pappus biseriate, the inner scales filiform, 4–5 mm long, persistent, the outer scales subulate, 0.5–1.0 mm long, persistent.

First described from Veraguas Province, *Vernonia seemanniana* is also known from the Province of Coclé. Although a poorly known species, this taxon is characterized by the many-floreted heads surrounded by long foliaceous bracts.

COCLÉ: Hills N of El Valle de Antón, *Allen & Allen 4179* (MO).

6. **Vernonia trifloscula**ta H.B.K., Nov. Gen. Sp. Pl. 4: 40. 1820. TYPE: Mexico, not seen.

V. triantha Schauer in Nees & Schauer, Linnaea 19: 714. 1847.
*Cacalia trifloscula*ta (H.B.K.) Kuntze, Rev. Gen. Pl. 2: 971. 1891.
Vernonia luxensis Coult., Bot. Gaz. (Crawfordsville) 20: 41. 1895.
V. dumeta Klatt, Bull. Soc. Roy. Bot. Belgique 35: 277. 1896.
*Eremosis trifloscula*ta (H.B.K.) Gleason, Bull. New York Bot. Gard. 4: 233. 1906.

Shrubs or small *trees* to 8 m high, lignescent, freely branched to form a rounded crown; branches erect to slightly spreading, striate, sparsely pubescent, cinereous, glabrescent. *Leaves* short-petiolate; petiole 0.8–1.5 cm long, canaliculate above; blades narrowly elliptic to broadly oblanceolate, acute to short-acuminate at the apex, acute to attenuate at the base, 5–12 cm long, 1–3 cm broad, marginally entire to minutely denticulate, plane and glabrous above, glabrate beneath, lateral veins ascending, 4–8 pairs, prominent beneath. *Inflorescences* terminal, forming a large hemispheric compound corymb. *Heads* with 3–4 florets, sessile to subsessile; involucre cylindric to narrowly campanulate, 2.5–6 mm long, 4–6-seriate, the outer involucral bracts subrotund, obtuse or apiculate at the apex, scarious, the inner involucral bracts oblong to ovate, acute to acuminate at the apex, scarious; receptacle subconvex, alveolate, naked; corolla narrowly cylindric, 5–6 mm long, 5-lobed, the lobes subulate, 1–1.5 mm long; stamens 5, the anthers 2–2.5 mm long, apically acute, basally obtusely sagittate; styles 5–6 mm long, the branches 1–2 mm long, apically acute, antrorsely puberulous. *Achenes* narrowly turbinate,

8–10-ribbed, antrorsely puberulent, 2.5–3 mm long; pappus weakly biseriate, white, the inner bristles capillary, 4.5–6 mm long, the outer bristles subulate to capillary, less than 1 mm long, persistent.

The only species of *Vernonia* in Panama with only three or four florets per head, *Vernonia triflosculosa* is known from a single collection in western Panama. The Panamanian specimen belongs to subspecies *triflosculosa* which extends from Panama throughout Central America to southern Mexico. Subspecies *palmeri* (Rose) Jones is restricted to western Mexico and is characterized by narrowly lanceolate leaves as opposed to broadly lanceolate to oblanceolate leaves of subspecies *triflosculosa*. Until recently, this species has been placed in the genus *Eremosis*.

CHIRIQUÍ: Boquete, *Davidson 642* (F, MO, US).

B. ELEPHANTOPODINAE

PHILIP BUSEY[6]

Elephantopodinae Less., Linnaea 5: 135. 1830. "Elephantopeae." TYPE: *Elephantopus* L.

Lychnophorinae Benth. in Benth. & Hook. f., Gen. Pl. 2: 171. 1873. "Lychnophorieae." TYPE: *Lychnophora* Mart.

6. ELEPHANTOPUS

Elephantopus L., Sp. Pl. 814. 1753; Gen. Pl., ed. 5. 355. 1754. TYPE: *E. scaber* L.

Orthopappus Gleason, Bull. New York Bot. Gard. 4: 237. 1906. TYPE: *E. angustifolius* Swartz.

Erect, perennial *herbs*; stems generally solitary. *Leaves* basal or cauline, alternate, basally attenuate, pinnately veined; petioles indistinct. *Inflorescences* solitary, terminal, bracteate panicles, spikes, or racemes, the heads in glomerules, the glomerules many-headed, hemispheric, subtended by 1 or more bracts. *Heads* with 2–4 florets; involucral bracts 8, similar, in 2 decussate series; receptacle convex, naked; flowers perfect, zygomorphic; corolla tubular-funnelform, the tube slender, the limb 5-parted, deeply so on the adaxial side; anthers 2-celled, sagittate at the base, apically appendaged; style branches slender, terete, slightly flattened adaxially at the base, strigulose throughout. *Achenes* obovoid, slightly flattened, 10-ribbed or -angled, strigulose or hispidulous; pappus in 1 series, occasionally scale-like, or usually of 5-many straight, equal, puberulent bristles.

A genus of 25 species centered around the Caribbean but ranging throughout the tropics and warmer temperate regions of both hemispheres; absent from Europe.

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Literature:

Clonts, J. A. 1972. A revision of the genus *Elephantopus*, including *Orthopappus* and *Pseudelephantopus* (Compositae). Ph.D. thesis, Mississippi State University.

a. Inflorescence paniculate; pappus bristles fewer than 10.
b. Leaves less than 3½ times longer than wide, densely soft-puberulent beneath ..... 3. *E. mollis*
bb. Leaves more than 7 times longer than wide, not densely soft-puberulent beneath ..... 2. *E. dilatatus*
aa. Inflorescence spicate, simple or sparingly branched; pappus bristles more than 20 ..... 1. *E. angustifolius*

1. **Elephantopus angustifolius** Swartz, Nov. Gen. Sp. Pl. Prodr. 115. 1788. Based on Sloane, Voy. Isl. Madera 1: 256, *pl. 148*, *fig. 4*. 1707.—FIG. 7E.

Orthopappus angustifolius (Swartz) Gleason, Bull. New York Bot. Gard. 4: 237. 1906.

Perennial subacaulescent *herbs*, mostly 30–120 cm tall with a short rootstock. *Leaves* crowded near the base forming a rosette, oblanceolate-oblong, basally long-attenuate, apically rounded-acute, sparsely crenate, 5–50 cm long, 1–3.5 cm wide, at least 3½ times longer than wide, coriaceous, green throughout, appressed-pubescent with somewhat silvery strigose trichomes, the trichomes 0.3–0.6 mm long on the lamina above (longer on the veins), 0.5–1.0 mm long beneath, inconspicuously veined above; petioles obscure, expanded and clasping at the base. *Inflorescence* solitary, spicate, simple or sparingly branched, of many glomerules each subtended by one or more lanceolate bracts to 8 mm long; peduncles appressed-pubescent; glomerules with ca. 20 heads, hemispheric, to 1.2 cm high and 2.5 cm wide. *Heads* with 4 florets; involucral bracts 8, similar, in 2 decussate series, minutely sericeous, the outer 4 ovate, 3–6 mm long, the inner 4 lanceolate-oblong, 6–10 mm long; corolla white to lavender, the tube slender, ca. 6 mm long, the limb ca. 2.0 mm long, deeply divided on the adaxial side, 5-parted, the lobes linear, ca. 1.6 mm long; anthers ca. 1.2 mm long, basally sagittate, the apical appendages 0.08–0.1 mm long; style branches slender, 0.5–0.8 mm long. *Achenes* obovoid, slightly flattened, 10-ribbed, 1.9–2.2 mm long, 0.5–0.6 mm wide, dark-brown, strigulose or hispidulous; pappus of 25–40 straight bristles in 1 series, the bristles 6.0–7.5 mm long, gradually dilated at the base to 0.12 mm wide, appressed-puberulent.

Elephantopus angustifolius was placed in a separate genus, *Orthopappus*, primarily on the basis of the large number of pappus bristles in this species. However, there are various degrees of this tendency in other species of *Elephantopus*, and the segregation of *E. angustifolius* in a separate genus is not justified.

Elephantopus angustifolius is of occasional occurrence in open savannas from Vera Cruz and the West Indies south through Central and South America to northern Argentina and Uruguay. Although formerly known from a number of localities in Panama, it has in recent years been collected from only two localities,

Cerro Campana and Tocumen. It has been collected throughout the year, but principally in the dry season, from November to March.

CANAL ZONE: Ancón Hill, *Greenman & Greenman 5115* (MO). Cerro Ancón, *Heriberto 47* (US). Ancón Hill, *Standley 25184* (US). Ancón Hill, *Standley 26319* (MO, US). CHIRIQUÍ: Between El Boquete and Caldera, 300–700 m, *Pittier 3338* (US). COCLÉ: Between Porto Posada and Penonomé, *Williams 157* (NY). PANAMÁ: Isla Taboga, *Allen 1274* (GH, MO). Between Panama and Chepo, *Dodge et al. 16657* (MO). Cerro Campana, *Duke 5964* (GH, MO). Tocumen, *Dwyer 4400* (FSU). Cerro Campana, *Ebinger 943* (GH, MO, US); *Lazor 3347* (FSU). Taboga Island, *Macbride 2840* (GH, US). Sabanas, *Paul 344* (US). Tocumen, *Standley 26501, 29400* (both US). Arraiján, *Woodson et al. 1389* (GH, MO, NY, US).

2. **Elephantopus dilatatus** Gleason, Bull. New York Bot. Gard. 4: 240. 1906. TYPE: Costa Rica, Buenos Aires, bords du Río Ceibo, *Pittier 3733* (US, isotype).

Perennial *herbs* mostly to 40 cm tall; stems creeping at the base, rooting at the nodes, enclosed in an overlapping series of persistent leaf sheaths, the sheaths pilose. *Leaves* clustered, terminal, oblanceolate-oblong, basally long-attenuate, apically acute, serrate, 7–18 cm long, 0.6–2.2 cm wide, at least 7 times longer than wide, coriaceous, green throughout, darker above, strigulose to appressed-pubescent beneath, the trichomes 0.2–1.3 mm long on both surfaces, resin-dotted beneath, the midrib prominent on both surfaces but the primary lateral veins obscure above; petioles pilose, indistinct from the lamina, expanded, clasping. *Inflorescence* solitary, terminal, corymbose-paniculate, the branches subtended by oblong leaflike bracts to 6 cm long, peduncles appressed-pubescent; glomerules several to many, 10–15-headed, hemispheric, to 8 mm high and 15 mm across, subtended by 2 or 3 ovate bracts; bracts obtuse at base, acute to acuminate, 5–8 mm long, the venation usually apparent but not conspicuous beneath. *Heads* with 4 florets; involucral bracts 8, in 2 decussate series, strigulose, resin-dotted, the outer 4 lanceolate, 3.0–4.5 mm long, the inner 4 lanceolate-oblong, 5.0–8.0 mm long; corolla lavender, the tube slender, ca. 3.5 mm long, the limb ca. 2.0 mm long, deeply divided on the adaxial side, 5-parted, the lobes linear, ca. 1.4 mm long; anthers ca. 1.2 mm long, basally sagittate, the lobes slightly convex, ca. 0.14 mm long, the apex forming a 25° angle, the apical appendage rounded, ca. 0.18 mm long; style branches slender, terete, slightly flattened adaxially, 0.5–1.0 mm long, strigulose throughout. *Achenes* obovoid, slightly flattened, 10-ribbed, 2.2–3.0 mm long, 0.6–0.8 mm wide, dark-brown in the sulci when mature, pale on the ribs, strigulose and resin-dotted abaxially; pappus in 1 series of 5(–8) straight bristles, 3.0–3.5 mm long, abruptly or gradually dilated to 0.3 mm wide at the base, appressed-puberulent.

Elephantopus dilatatus is similar to the Brazilian *E. riparius* Gardn. which differs chiefly in having much shorter bracts (less than 4 mm long) subtending the glomerules. *Elephantopus dilatatus* is known from Costa Rica, Panama, and the Chocó of Colombia (*Duke 9971*, OS). It occurs chiefly in riverine habitats and has been collected in Panama only in December and January.

CANAL ZONE: Quebrada La Palma and Cañon of Río Chagres, 70–80 m, *Dodge & Allen 17383* (MO, NY). COLÓN: Ca. 2–3 mi up the Río Guanche, ca. 10–20 m, *Kennedy & Foster 2140* (MO, PMA, US). PANAMÁ: Between Cerro Azul and Cerro Jefe, *Dressler 3269* (DUKE, FSU, MO).

3. **Elephantopus mollis** H.B.K., Nov. Gen. Sp. Pl. 4: 26. 1820. TYPE: Caracas, *Herb. Humboldt & Bonpland 627* (P, not seen, IDC 6209. 91. I, 1).—FIG. 7A–D.

E. carolinianus var. *mollis* (H.B.K.) Beurl., Bidr. Portobellensis Fl. 134. 1854.
E. hypomalacus Blake, Contr. Gray Herb. 52: 20. 1917. TYPE: Costa Rica, *Holway 314* (GH, not seen).

Coarse perennial *herbs* mostly 30–150(–200) cm tall, occasionally from a creeping rootstock; stem erect, leafy, usually hollow, villous, the trichomes to 1.5 mm long. *Leaves* cauline, rarely basal, more or less oblanceolate, basally attenuate, apically acute, crenate, mostly 7–22 cm long, 2–7 cm wide, less than 3½ times longer than wide, chartaceous, green throughout, darker above, resin-dotted and densely soft-puberulent beneath, the trichomes to 0.5 mm long, slightly longer on the veins, above muricate and sparsely appressed-pubescent, somewhat obscurely veined above; petioles broadly expanded at the base, clasping. *Inflorescence* solitary, terminal, a much-branched corymbose panicle, the branches subtended by oblong leaflike bracts to 6 cm long; peduncles appressed-pubescent; glomerules many, with ca. 40 heads, hemispheric, to 10 mm high and 20 mm across, subtended by 2 or 3 ovate bracts; bracts obtuse at base, slightly acuminate, 6–12 mm long, the venation arcuate-ascending, conspicuous beneath, obscure above. *Heads* with 4 florets; involucral bracts 8, in 2 decussate series, minutely sericeous towards the apex, usually resin-dotted, the outer 4 lanceolate, 4.5–5.0 mm long, the inner 4 lanceolate-oblong, acuminate, 5.5–7.5 mm long; corolla white or occasionally pinkish, the tube slender, 3.0–4.0 mm long, ca. 0.15 mm wide, the limb ca. 2.0 mm long, deeply divided on the adaxial side, 5-parted, the lobes linear, ca. 1.2 mm long, ca. 0.18 mm wide; anthers ca. 1.0 mm long, ca. 0.18 mm wide, basally sagittate, 0.12–0.15 mm long, the apical appendage ca. 0.1 mm long; style branches slender, terete, somewhat flattened adaxially, ca. 0.7 mm long, strigulose throughout, but less densely on the adaxial surfaces. *Achenes* obovoid, slightly flattened, 10-ribbed, 1.9–2.7 mm long, ca. 0.7 mm wide, brown in the sulci when mature, pale on the ribs, strigulose and resin-dotted; pappus in 1 series of 5(–8) straight bristles, 3.5–4.7 mm long, abruptly or somewhat gradually dilated at the base, to 0.25 mm wide, the dilated portion 0.2–0.6 mm long, the bristles appressed-puberulent, often ciliate at the base.

At high elevations *Elephantopus mollis* assumes a dwarfed, rosette-type habit, and such forms have been mistaken for the Old World *E. scaber* L. The latter is distinguished by its stiff, coriaceous, oblong-oblanceolate leaves that are not soft-puberulent beneath. In Mexico, *E. mollis* overlaps with and perhaps intergrades with the temperate *E. tomentosus* L. The latter is distinguished by leaves

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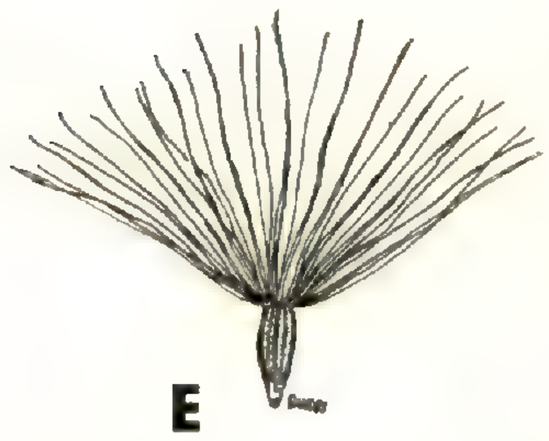
FIGURE 7. *Elephantopus*.—A–D. *E. mollis* H.B.K.—A. Habit (× ½). [After *Busey 329* (MO).]—B. Floret (× 2½). [After *Porter et al. 4642* (MO).]—C. Achene (× 2½). [After *Johnston 1061* (MO).]—D. Head (× 2½). [After *Croat 13016* (MO).]—E. *E. angustifolius* Swartz. Achene (×2½). [After *Woodson et al. 1389* (MO).]


E
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BUSEY
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R.J. White

that are appressed-pubescent beneath with trichomes ca. 1 mm long, and by achenes that are at least 4 mm long.

The soft-puberulence on the undersides of the leaves of *Elephantopus mollis* is a distinctive character and, when used to separate *E. mollis* from related taxa, is well correlated with achene size and geographic distribution. Thus, it is useful to recognize this taxon at the species level. Earlier workers have, however, considered *E. mollis* at infraspecific levels under other names, e.g., *E. scaber* var. *tomentosus* (L.) Baker sensu Baker in Mart., Fl. Bras. 6(2): 173, and *E. tomentosus* var. *carolinianus* (Raeusch. not Willd.) Schultz-Bip. sensu Schultz-Bip., Linnaea 20: 516. 1847. Furthermore, *E. mollis* demonstrates throughout its range all degrees of variation in the abruptness of dilation of the pappus bristles, and the segregation of forms with very gradually dilate pappus bristles, as *E. hypomalacus* Blake, is unjustified.

Elephantopus mollis is pantropical. In Panama it is widespread, particularly in more protected habitats along roadsides, in pastures, and on forest margins. It flowers almost exclusively from December to March. Names for this species include "yerba de caballo" (Colombia), "lengua de vaca" (Puerto Rico), and "cucha-cara" (Peru).

BOCAS DEL TORO: Almirante, *Blum 1310* (FSU, MO). Changuinola Valley, *Dunlap 319* (GH, US). CANAL ZONE: 15 mi from Gamboa, *Blum 2046* (FSU, MO). 10 km N of Gamboa, *Busey 329* (DUKE, ENCB, FSU, MO, PMA, US, WIS). Cerro de Ancón, *Celestine 88* (US). Pipeline Road, *Correa & Haines 542* (DUKE, FSU, MO). Barro Colorado Island, *Croat 7787, 13155* (both MO). Madden Forest, *Croat 8936* (MO). Near Summit, *Croat 9070* (MO). Chagres, *Fendler 163* (MO, US). Ancón Hill, *Greenman & Greenman 5093* (MO). Gatún, *Hayes 677* (NY). W of Thatcher Ferry Bridge, *Lazor 2187* (MO). Ancón, *Macbride & Featherstone 15* (US); *Piper 5581* (US). *Standley 26341* (US). Balboa, *Standley 26975* (US). Corozal, *Standley 27381* (US). Gamboa, *Standley 28509* (US). Mount Hope Cemetery, *Standley 28765* (US). Between Ft. Clayton and Corozal, *Standley 29045* (US). Balboa, *Standley 29247, 32101* (both US). Between France Field and Cativa1, *Standley 30282* (US). Near Ft. Sherman, *Standley 31047* (US). Obispo, *Standley 31655* (US). Pipeline Road, *Wilbur & Weaver 11261* (DUKE); *Wilbur & Teeri 13355* (DUKE). 1 mi SW of Cocolí, *Wilbur et al. 12916* (DUKE). CHIRIQUÍ: 17.5 km N of Paso de Canoa, *Busey 618* (DUKE, ENCB, GH, MO, PMA, NY, OS, US). Boquete, 4000 ft, *D'Arcy & D'Arcy 6469* (C, F, MO). Bajo Mono, Boquete, 3800 ft, *Davidson 600* (GH, MO). Volcán, 4600 ft, *Duke 9200* (MO). Near Volcán, 600–750 m, *Graham s.n.* (GH). 1 mi S of Volcán, *Lazor & Correa 2759* (FSU, MO). Near Boquete, 3300–4200 ft, *Lewis et al. 626* (GH, MO, US). 14 mi N of David, 1200 ft, *Lewis et al. 688* (GH, MO). 2.2 mi E of El Hato del Volcán, *Luteyn 809* (DUKE, MO). Alto Boquete, 1125 m, *Partch 69–84* (MO). 2.5 mi W of El Hato del Volcán, *Wilbur et al. 15103* (DUKE). COCLÉ: 3 mi NE of Antón, *Croat 9619* (MO). Near El Valle de Antón, *Croat 13289* (MO). Cerro Pilón near El Valle, 700–900 m, *Duke 12115* (MO, OS). 3–4 mi N of El Valle, *Gentry & Dwyer 3604* (MO). S of El Valle, 600 m, *Gentry 6804* (MO). About 2 mi W of Natá, *McDaniel & Tyson 14703* (FSU). Foot of Cerro Pilón, 2000 ft, *Porter et al. 4642* (MO). Ca. 3 mi N of El Valle, 650 m, *Wilbur et al. 15679* (DUKE). COLÓN: 5–7 mi SW of Portobelo, *Wilbur & Weaver 11172* (DUKE). DARIÉN: Manené, *Kirkbride & Bristan 1593* (MO). HERRERA: Near Ocú, 100 m, *Allen 4050* (GH, MO). LOS SANTOS: 16 mi S of Macaracas at Quebrada Bejuco, *Tyson et al. 3099* (MO). PANAMÁ: 7 mi N of Cerro Azul, 2600 ft, *Blum et al. 1847* (FSU). Beyond Goofy Lake, *Correa & Dressler 549* (DUKE, FSU, MO, OS). 2 mi above Goofy Lake, *Croat 13016* (MO). Cerro Jefe to La Eneida, *Duke & Dressler 8240* (MO). Cerro Azul, *Duke 9362* (MO, OS); *Dwyer & Gentry 9523* (MO, NY). Capira, trail between Lidice and Aguacate, 200 m, *Foster 2144* (DUKE). Llanos de Panamá Viejo, *Heriberto 291* (GH, NY, US). Near Chepo, 30 m, *Hunter & Allen 34* (MO), *60* (GH, MO, NY). San José Island, *Johnston 1061* (GH, MO, US). 2–3 mi S of Goofy Lake, 2000–2200 ft, *Lewis et al. 241* (MO). Chimán, *Lewis et al. 3362* (MO). Sabanas, *Macbride 2631* (US). Sabanas N of Panama City, *Paul 420* (US). Near Bella Vista, *Piper 5392* (US). Cerro Azul, *Porter et al. 4077* (DUKE, MO, NY). Nuevo San Francisco, *Standley 30785* (US). Between

Las Sabanas and Matías Hernández, *Standley 31874* (US). 9 km SE of El Valle de Antón, *Wilbur et al. 11164* (DUKE). VERAGUAS: Hills W of Soná, 500 m, *Allen 1026* (GH, MO, US). Montijo, 8 mi S of Santiago, *Tyson 6037* (FSU, MO).

7. PSEUDELEPHANTOPUS

Pseudelephantopus Rohr, Skr. Naturhist.-Selsk. 2: 213. 1792. "PseudoElephantopus." TYPE: *Elephantopus spicatus* Juss.

Distreptus Cass., Bull. Soc. Philom. 1817: 66. 1817. TYPE: *Elephantopus spicatus* Juss.
Spirochaeta Turcz., Bull. Soc. Imp. Naturalistes Moscou 24: 166. 1851. TYPE: *S. funckii* Turcz.
Chaetospira Blake, Jour. Wash. Acad. Sci. 25: 311. 1935. TYPE: *Spirochaeta funckii* Turcz.

Erect, perennial *herbs*; stems solitary, branched. *Leaves* cauline, alternate, pinnately veined; petioles indistinct. *Inflorescences* several, terminal, racemose-spicate, the heads clustered in the axils of leaflike bracts, the clusters 1–several-headed, obconic. *Heads* with 4 florets; involucral bracts 8, similar, in 4 decussate pairs, abaxially bicolored; receptacle naked, convex, bearing minute protuberances at the base of the achenes, florets bisexual, zygomorphic; corolla tubular-funnelform, the tube slender, the limb 5-cleft, deeply divided on the adaxial side; anthers 2-celled, sagittate at the base, apically appendaged; style bifid, the branches slender, flattened and stigmatic adaxially, strigulose abaxially. *Achenes* ± obovoid, slightly flattened, 10-ribbed, hispidulous or strigulose primarily on the ribs; pappus in 1 series of 5–10 unequal or subequal bristles, doubly bent or spiralled toward the apex, glabrous on the surfaces, ciliolate.

A neotropical genus of 2 species, both of which are known from Panama. Cronquist (1971) gives reasons supporting the spelling *Pseudelephantopus*.

Pseudelephantopus is conspicuously different from all members of *Elephantopus* in the general construction and appearance of the inflorescence. The heads of *Pseudelephantopus* are not densely held in a tight glomerule, and the subtending bracts are not highly specialized as in *Elephantopus*, but are leaflike. Furthermore, *Pseudelephantopus* differs cytologically. *Pseudelephantopus spicatus* has been reported (Cronquist, 1971) to have $2n = 28$, in contrast to *Elephantopus*, which has $2n = 22, 44$ (Federov, 1969).

Literature:

Cronquist, A. 1971. Compositae. Pp. 350–353 *in* I. L. Wiggins & D. M. Porter, Flora of the Galapagos. Stanford Univ. Press, Stanford, California.

a. Principal pappus bristles conspicuously doubly bent; achenes more than 5 mm long ..... 1. *P. spicatus*
aa. Pappus bristles curled or loosely spiralled; achenes less than 5 mm long ..... 2. *P. spiralis*

1. **Pseudelephantopus spicatus** (Juss.) C. F. Baker, Trans. Acad. Sci. St. Louis 12: 55. 1902.—FIG. 8A–C.

Elephantopus spicatus Juss. in Aublet, Hist. Pl. Guiane 2: 808. 1775. Based on Sloane, Voy. Isl. Madera 1: 256, *pl. 150, fig. 3–4*. 1707.
Distreptus spicatus Cass. in Levr., Dict. Sci. Nat. 13: 367. 1819.

Erect, mostly perennial *herbs* or *subshrubs* 10–60(–120) cm tall, often arising from a creeping rootstock; stem striate, sometimes hollow, the branching dichot-

omous, ascending, the branches to 30 cm long, strigose, with trichomes 1.0–1.8 mm long. *Leaves* cauline, the lower oblanceolate, basally attenuate, acute at apex, sinuate or more commonly sparsely serrate, 4–21 cm long, 2–6 cm wide, chartaceous, strigose and resin-dotted beneath, merely hispid above, the pubescence at first dense, becoming sparse with age, the trichomes 0.8–1.8 mm long, the leaves becoming shorter and more oblong-elliptic upwards and merging into the bracts of the inflorescence, venation somewhat obscure above; petioles indistinct, winged, the blades essentially sessile. *Inflorescences* several racemose-spicate branches, the nodes with ± elliptic, leaflike bracts to 3 cm long, generally 5–20 mm apart; clusters of heads subsessile, solitary in the axils, scorpioid, conical, to 15 mm high and 10 mm across, loose, few-headed, the individual heads overlapping but distinguishable; bracteoles oblong, to 2 cm long. *Heads* with 4 florets; involucral bracts 8, similar, in 4 decussate pairs, the outer pairs progressively shorter, the inner 2 pairs subequal, oblong-oblanceolate, boat-shaped, 8–10 mm long, 1.5–2.0 mm wide, mucronate, keeled, glabrescent, green towards the apex, hyaline basally, on the keel, and along the margins; corolla white or lavender, the tube slender, 5–6 mm long, the limb 3–4 mm long, deeply divided on the adaxial side, 5-cleft, the lobes ca. 2 mm long; anthers ca. 1.5 mm long, basally sagittate, the lobes ca. 0.15 mm long, the apical appendage rounded, ca. 0.16 mm long; style branches flattened and stigmatic adaxially, ca. 1.2 mm long, strigulose on the abaxial side of the branches and for ca. 0.4 mm on the shaft apex. *Achenes* narrowly obovoid, slightly flattened, 10-ribbed, 5.5–7 mm long, ca. 1 mm wide at the apex, tapered to the base, hispidulous principally on the ribs, the trichomes ca. 0.2 mm long, usually resin-dotted principally between the ribs; pappus in 1 series of 6–10 bristles, with the 2 lateral bristles longest, 4–6 mm long, gradually dilated to 0.3 mm wide at the base, and conspicuously doubly bent for about 1 mm, and with 2 abaxial bristles longer than the others, 3–5 mm long, generally straight, the remaining 1–3 pairs shorter and less conspicuous, the bristles generally lacerate at the base.

Pseudelephantopus spicatus ranges throughout tropical Mexico, the West Indies, south throughout Central America and northern South America, including Peru; it is also reported from Chile. The species has been introduced to East Asia and the Pacific, and has recently been collected in West Africa. It is extremely common in pastures and clearings throughout Panama, and flowers almost exclusively between December and April.

In Panama this species is usually called "chicoria" or "suelda consuelda," but is also called "escobilla blanca." Elsewhere (El Salvador) *Pseudelephantopus spicatus* is called "oreja de perro" or "oreja de chucho." A syrup from the plant is used to cure coughs; it is also used to make brushes and brooms. According to the information on *Duke 10849* (San Blas), *P. spicatus* is called "candeabsurguit" and is "taken by [the] Cuna in the belief that it is vitamin rich." Information from *Lazor & Correa 3383* (Darién) indicates the species may be believed to be useful in worming cattle.

BOCAS DEL TORO: Talamanca Valley, *Carleton 107* (GH, US). Almirante, *Cooper 143* (GH, US). Changuinola Valley, *Dunlap 294* (US). Near Changuinola, *Lewis et al. 831* (GH, MO, NY). Near Chiriquicito, *Lewis et al. 2100* (ENCB, GH, MO). CANAL ZONE: Barro

FIGURE 8. *Pseudelephantopus*.—A–C. *P. spicatus* (Juss.) C. F. Baker.—A. Habit (× ½). —B. Achene (× 5).—C. Head (× 5). [After *Busey 457* (MO).]—D. *P. spiralis* (Less.) Cronq. Achene (× 5). [After *Croat 7510*, Colombia (MO).]

Colorado Island, *Bailey & Bailey 116* (GH). Ft. San Lorenzo, *Burch et al. 1023* (GH, MO, NY). Barro Colorado Island, *Croat 4084, 4161, 4168, 6911, 8565* (all MO). Madden Forest, *Croat 12894* (MO). Río Azote Caballo, 66–70 m, *Dodge et al. 16858* (MO). Las Cruces Trail, *Dwyer 1962* (MO). Chagres, *Fendler 175* (MO, US). Madden Forest, *Flórez 56* (DUKE,

MO). Ancón, *Greenman & Greenman 5004* (GH, MO). Gatún, *Hayes 476* (GH, NY, US). Pedro Miguel, *Heriberto 45* (GH, NY). Near Arraiján, *Lewis et al. 5185* (MO). Ancón, *Macbride & Featherstone 14* (US). Empire to Mandinga, *Piper 5504* (GH, US). Near Madden Dam, *Porter et al. 4030* (MO, US). Gamboa, *Porterfield s.n.* (NY). Balboa Station, *Porterfield s.n.* (NY). Sosa Hill, *Standley 26456* (GH, US). Near Summit, *Standley 29533* (GH, US). Darién Station, *Standley 31579* (US). Near Gatún Station, *Tyson 2277* (MO). Ft. San Lorenzo, *Tyson & Blum 3694* (FSU, MO). Near Cocolí, *Wilbur et al. 12904* (DUKE, MO). CHIRIQUÍ: San Bartolo Límite, *Busey 457* (ENCB, MO). Rabo de Puerco, *Liesner 35* (MICH, MO, NY). Quebrada Melliza, *Liesner 427* (F, MO). Río Fonseca, *McCorkle C-72* (FSU). COCLÉ: Río Grande, *Burch et al. 1173* (GH, MO, NY). El Valle de Antón 1000–2000 ft, *Lewis et al. 2592* (DUKE, GH, MO). El Cope, 1500 ft, *Tyson 5203* (DUKE, FSU, MO). COLÓN: Santa Rita, *Kennedy 2766* (F, MO, NY, UC, MICH). DARIÉN: Río Piñas, *Duke 10567* (MO, OS). Río Pirre, *Kennedy 2873* (C, F, MO, NY). Yaviza, *Lazor & Correa 3383* (FSU). LOS SANTOS: Río Pedregal, *Lewis et al. 2977* (MO). PANAMÁ: Isla Taboga, *Allen 1299* (GH, MO). Isla del Rey, *Duke 9503* (MO, OS). Tocumen, *Dwyer 4118 A* (MO). San José Island, *Johnston 971* (GH). Chimán, *Lewis et al. 3313* (MO). Old Panama, *Porterfield s.n.* (NY). Taboga Island, *Standley 27095, 27835* (both US), Saboga Island, *Tyson & Loftin 5146* (DUKE). Chilibre, *Tyson & Lazor 6107* (FSU). SAN BLAS: Permé, *Cooper 257* (NY, US). Río Ailigandí, *Duke 10849* (MO, OS). Ailigandí, *Lewis et al. 68* (GH, MO).

2. **Pseudelephantopus spiralis** (Less.) Cronq., Madroño 20: 255. 1970.—FIG. 8D.

Distreptus spiralis Less., Linnaea 6: 690. 1831. TYPE: Jamaica, *Herb. Thunberg 20920* (UPS, not seen, IDC 1036. 878. I, 4).

Spirochaeta funckii Turcz., Bull. Soc. Imp. Naturalistes Moscou 24: 167. 1851. TYPE: Venezuela, La Guayra, *Funck 358*, Galeotti Herb. 380 (G-Delessert Herb. 28530, not seen, MO, US, photos).

Chaetospira funckii (Turcz.) Blake, Jour. Wash. Acad. Sci. 25: 311. 1935.

Pseudelephantopus funckii (Turcz.) Philipson, Jour. Bot. 76: 301. 1938.

Erect, perennial stoloniferous *herbs* 10–80 cm tall; stem sometimes hollow, the branches few, ascending, generally with one branch distinctly dominant, the branches to 35 cm long, hispid, with trichomes 1.3–2.5 mm long. *Leaves* cauline, the lower obovate to oblanceolate, basally cuneate, acute or sometimes rounded at apex, sinuate and sparsely serrate, 2–7(–14) cm long, 1.2–2.0(–4.5) cm wide, chartaceous, resin-dotted beneath when young, merely punctate later, hispid or sometimes strigose on both surfaces, the pubescence at first yellowish, later whitish, persistent, the trichomes 2.0–3.5 mm long, shorter in depauperate individuals, the leaves becoming abruptly shorter, oblong-elliptic upwards; venation somewhat obscure above; petioles winged, basally broadly expanded, apically constricted. *Inflorescences* several racemose-spicate branches or solitary, the flowering nodes with oblong bracts mostly to 1.5 cm long, 2–10 mm apart; clusters of heads subsessile, solitary in the axils, generally overlapping, capitate, obconic, to 9 mm high and 12 mm across, dense, 5–10-headed, the individual heads overlapping and ± distinguishable. *Heads* with 4 florets; involucral bracts 8, similar, in 4 decussate pairs, the outer pairs progressively shorter, the inner 2 pairs subequal, oblong-lanceolate, boat-shaped, 7–8 mm long, 1–2 mm wide, mucronate, not keeled, scabridulous and somewhat greener toward the apex, hyaline basally and along the margins; corolla blue-violet, the tube slender, ca. 3.5 mm long, the limb ca. 2.5 mm long, deeply divided on the adaxial side, 5-parted, the lobes ca. 1 mm long; anthers ca. 1.2 mm long, basally sagittate, the lobes ca. 0.15 mm long, apically appendaged; style branches flattened and stigmatic adaxially, ca. 1.0 mm long, minutely strigulose on the abaxial side of the branches and slightly

below the dichotomy. *Achenes* obovoid, slightly flattened, 10-ribbed, 2.5–3.3 mm long, ca. 0.8 mm wide, strigulose, the trichomes 0.1 mm long, usually resin-dotted; pappus in 1 series of 5–10 bristles of approximately equal length, curled or loosely spiralled toward the apex, usually slender throughout, rarely to 0.3 mm wide at the base.

Pseudelephantopus spiralis occurs in fields and waste areas, particularly near streams and marshes from Costa Rica and the Lesser Antilles throughout northern South America and along the eastern slope of the Andes to Bolivia and northern Argentina. Although rare in Panama, this species is common in Colombia, where it is called "suelda con suelda."

DARIÉN: Manené, *Kirkbride & Bristan 1570* (MO, PMA). VERAGUAS: Mouth of Río Concepción, *Lewis et al. 2775* (MO, OS, PMA).

8. ROLANDRA

Rolandra Rottb., Collect. K. Medic (Copenhagen) 2: 256. 1775. TYPE: *Echinops fruticosus* L. = *Rolandra fruticosa* (L.) Kuntze.

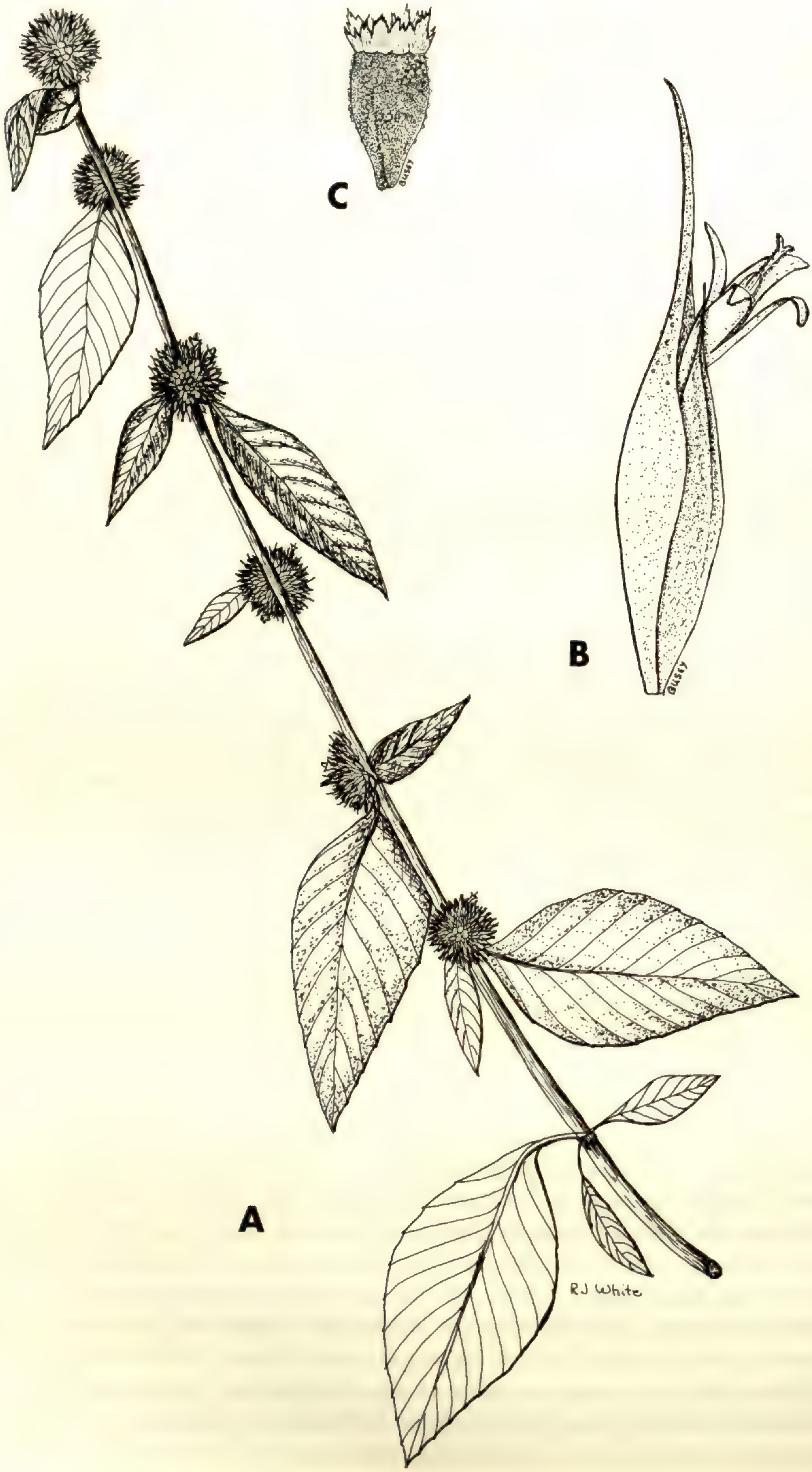
Decumbent perennial *herbs* or *subshrubs*. *Leaves* cauline, alternate, conspicuously white-tomentose beneath, not basally attenuate, venation pinnate; petioles distinct. *Inflorescences* several, solitary, terminal and axillary glomerules; glomerules many-headed, globose, ebracteate. *Heads* with 1 floret; involucral bracts coriaceous, 2(3), alternate; receptacle obsolete; florets bisexual, actinomorphic; corolla tubular-campanulate, the tube slender, the limb 4-parted; anthers basally sagittate, apically appendaged; style branches short, strigulose abaxially. *Achenes* obovoid, slightly flattened, glabrous, smooth but resin-dotted, obscurely 5-nerved; pappus in 1 series, a short, continuous crown of scales.

The genus is monotypic.

1. **Rolandra fruticosa** (L.) Kuntze, Rev. Gen. Pl. 1: 360. 1891.—FIG. 9.

Echinops fruticosus L., Sp. Pl. 815. 1753. TYPE: not seen.
Rolandra argentea Rottb., Collect. K. Medic (Copenhagen) 2: 256. 1775. Based on Sloane, Voy. Isl. Madera 1: 47, *pl.* 7. 1707.
Echinops nodiflorus Lam., Encycl. Meth. 2: 337. 1786. TYPE: Guyana, Cayenne, (P-LA, not seen, IDC 6207. 366. I, 6).

Decumbent perennial *herbs* or *subshrubs* to 150 cm long, sparingly branched; stems solid, to 7 mm in diameter, brown, white-sericeous. *Leaves* distributed along the stem, lanceolate-elliptic, basally rounded-obtuse, apically somewhat acuminate, sparsely serrulate, 4–11 cm long, 1.5–5 cm wide, ± scarious, muricate-scabridulous above and sparsely sericeous when young, beneath conspicuously white-tomentose, secondary veins 9–12 pairs, prominent beneath, sunken above; petioles 5–15 mm long. *Inflorescences* dense glomerules, upper-axillary and terminal; glomerules 300–400-headed, essentially ebracteate, globose, 10–15 mm in diameter. *Heads* with 1 floret; involucral bracts mostly 2, alternate, lanceolate, boat-shaped, laterally compressed and somewhat keeled, coriaceous, more or less resin-dotted abaxially towards the apex and apically ciliolate, glabrescent, the outermost 5.0–6.5 mm long, with a sharp acumen ca. 1 mm long, the innermost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largely enclosed by the outer bract, ca. 4 mm long, a third, elongate, ca. 2 mm long, vestigial involucral bract sometimes present below the major ones; corolla white, the tube slender, 1.7 mm long, the limb 1.8 mm long, 4-parted, the lobes lanceolate, equal, 1.5 mm long, 0.5 mm wide at the base; anthers 1.0 mm long, basally sagittate, the lobes 0.08 mm long; style branches 0.2 mm long, flattened adaxially, strigulose abaxially. *Achenes* obovoid, slightly flattened, smooth, obscurely 5-nerved, 1.5 mm long, 0.8 mm across at the widest point, vitreous-yellow to -brown, resin-dotted throughout; pappus in 1 series, a continuous crown of many persistent somewhat lacerate, united hyaline scales 0.15–0.30 mm long.

Rolandra fruticosa ranges from Honduras southward, and from Puerto Rico and the Lesser Antilles throughout northern South America to Brazil; introduced to Japan and Java. In Panama it is widespread in grazed areas and moist thickets, principally from the Caribbean slope and moister aseasonal climates. It flowers principally from December to April. According to information on *Duke 10845* (San Blas, MO) *R. fruticosa* is called "niagurgin" and is "taken in teas by [the] Cuna in belief that it will increase their ability to make 'molas' rapidly."

BOCAS DEL TORO: Isla Colón, *Wedel 55* (GH, MO). CANAL ZONE: 15 mi N of Gamboa, *Blum 2042* (FSU, MO). Barro Colorado Island, *Busey 298* (ENCB, MO, PMA). Cerro de Ancón, *Celestine 65* (US). Barro Colorado Island, *Croat 4150, 4352, 7483, 7784, 8589* (all MO). Pipeline Road near Gamboa, *Croat 4694* (MO). Madden Forest, *Croat 8948* (MO). Far end of Pipeline Road, *Croat 12782* (MO, NY). Ft. Sherman, *Duke 4360* (MO). Chagres, *Fendler 143* (MO, US). Barro Colorado Island, *Foster 1441* (DUKE). Gatún Station, *Hayes 605* (NY). Gatún, *Heriberto 107* (US). Ancón Hill, *Piper 5574* (GH, NY, US). Near Old Ft. Lorenzo, *Piper 5969* (US). Between Río Grande and Pedro Vidal, *Pittier 2706* (NY, US). Barro Colorado Island, *Shattuck 419* (MO). Balboa, *Standley 25459* (US). Swampy woods near Ft. Randolph, *Standley 28607* (US). Between France Field and Cativa, *Standley 30311* (US). Barro Colorado Island, *Standley 40988* (US). N of Summit, *Tyson et al. 2782* (FSU, MO, NY). Ca. 8.5 mi NW of Gamboa, *Wilbur & Teeri 13419* (DUKE). CHIRIQUÍ: El Nancito, 700 ft, *Tyson 6392* (FSU, MO). COCLÉ: Between La Mesa and El Valle de Antón, *Wilbur & Luteyn 11686* (DUKE). Penonomé, *Williams 153* (NY, US). COLÓN: Río Chagres above Gamboa, *Allen 4137* (MO). La Represa, *Chan 41* (MO). Guasimo, *Croat 9976* (MO). Isla Grande, *D'Arcy 4024* (MO). Santa Rita Ridge, *D'Arcy & D'Arcy 6178* (MO). Santa Rita, N of Agua Clara rain gauge, *Kennedy 2766* (F, MICH, MO, NY, UC). Near Escobal, *McCorkle C-182* (FSU). Near Portobelo, *Nee & Mori 3646* (MO). Santa Rita, *Wilbur & Weaver 10827* (MO); *Wilbur et al. 15050* (DUKE). DARIÉN: Río Congo, *Bristan 653* (MO). HERRERA: Between Las Minas and Pesé, 900–1200 ft, *Burch et al. 1345* (MO, PMA). Near Las Minas, *Stern et al. 1767* (US). PANAMÁ: Cerro Jefe, 2700 ft, *Blum & Duke 2203* (FSU, MO). Cerro Azul, *Busey & Croat 254* (C, DUKE, ENCB, F, FSU, GH, K, LE, MO, NY, OS, P, PMA, UC, US, WIS). Near Cerro Azul, *D'Arcy & D'Arcy 6239* (MO). Cerro Azul, *Duke 9364* (MO, OS). Isla del Rey, *Duke 10414* (MO, OS). Cerro Azul, *Dwyer 1869* (MO). Near Goofy Lake, 2000 ft, *Dwyer 2073* (MO). Cerro Campana, 2600–2800 ft, *Lewis et al. 1949* (GH, MO). Bellevista, *Macbride 2739* (MO, US). Cerro Azul, *Porter et al. 4072* (MO). Cerro Jefe, *Porter et al. 5057* (MO). Cerro Azul, 2000 ft, *Tyson 2050* (MO). Cerro Jefe, 3000 ft, *Tyson et al. 4439* (FSU, MO). Cerro Azul, *Tyson & Lazor 6088* (FSU). Cerro Jefe, 2700–3000 ft, *Wilbur & Teeri 13634* (DUKE). SAN BLAS: Río Ailigandí, *Duke 10845* (MO). Ailigandí River, *Lewis et al. 82* (GH, MO, US). VERAGUAS: Río Concepción, *Lewis et al. 2792* (MO).

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FIGURE 9. *Rolandra fruticosa* (L.) Kuntze.—A. Flowering stem (× 7/10).—B. Head (× 13½). [After *Croat 7784* (MO).]—C. Achene (× 13½). [After *D'Arcy & D'Arcy 6239* (MO).]

9. SPIRACANTHA

Spiracantha H.B.K., Nov. Gen. Sp. Pl. 4: 28. 1820. TYPE: *S. cornifolia* H.B.K.

Erect or decumbent perennial *herbs*. *Leaves* cauline, alternate, conspicuously white-tomentose beneath, not basally attenuate, venation pinnate; petioles distinct. *Inflorescences* many terminal or pedunculate bracteate clusters of glomerules, the clusters capitate, subtended by leaflike, spine-tipped bracts; glomerules many, each a compact unit of several heads, each head tightly held by a broad, spine-tipped bract. *Heads* with 1 floret; involucral bracts membranous, 6, in 2 series; receptacle obsolete; florets bisexual, actinomorphic; corolla tubular-funnelform, the tube slender, the limb 4-parted; anthers basally sagittate, apically appendaged; style branches stigmatic adaxially, essentially naked. *Achenes* turbinate, semiterete, glabrous, smooth, obscurely 5-nerved, apically resin-dotted; pappus in more than 1 series of many slender scales.

The genus is monotypic.

The bract subtending and enclosing the head in *Spiracantha* is similar to the involucral bracts of *Rolandra*. The latter coriaceous bracts contrast strongly with the paleaceous involucral bracts of *Spiracantha*. In view of the fact that the two genera are otherwise similar and closely related, it is possible these organs are not homologous in *Rolandra* and *Spiracantha*.

1. **Spiracantha cornifolia** H.B.K., Nov. Gen. Sp. Pl. 4: 29. 1820. TYPE: Venezuela, ad portum Zapote, *Herb. Humboldt & Bonpland 1367* (P, not seen, IDC 6209. 91. I, 4).—FIG. 10.

Erect or partially decumbent *herbs* 30–150(–200) cm long; stems loosely branched, purplish on exposed areas, sericeous, the trichomes to ca 1.4 mm long. *Leaves* distributed along the stem, ± elliptic, basally obtuse, apically acute and sharply mucronate, serrulate, 2.5–11 cm long, 1–4 cm wide, chartaceous, sericeous above, beneath conspicuously white-tomentose, secondary veins 6–10 pairs, prominent beneath, sunken above; petioles 5–15 mm long, expanded-deltoid and basally clasping. *Inflorescences* capitate clusters; peduncles 1–10 cm long; clusters ca. 1.5 cm tall, 2.5–4 cm across, containing 20–25 subsessile glomerules, several of the lower glomerules arising from and tightly enclosed by a leaflike bract; bract ovate, to 2 cm long, membranous, with a sharp mucro ca. 1.5 mm long; the glomerules compact, 3–11-headed, 5–8 mm high, 5 mm across, with a strigulose bract subtending each head; bract ovate, keeled, with a sharp, horizontally directed mucro ca. 1.5 mm long. *Heads* with 1 floret; involucral bracts membranous, about 6, ± imbricate, linear, 4–4.5 mm long, conspicuously lanate at the base; corolla blue-violet, the tube slender, 1.4 mm long, the limb 1.6 mm long, 4-parted, the lobes equal, 1.0 mm long; anthers 0.9 mm long, basally sagittate, the appendage ca. 0.3 mm long; style branches 0.3 mm long, glabrate. *Achenes* turbinate, semiterete, smooth, 2 mm long, 0.7 mm across at the widest point, smooth, obscurely 5-nerved, vitreous-gray, resin-dotted in a ring around the top; pappus in 2 series, the outer series of 10 or more hyaline, minutely strigulose scales of different lengths, 0.5–1.0 mm long, the inner series considerably shorter, the scales linear-lanceolate, readily deciduous.

FIGURE 10. *Spiracantha cornifolia* H.B.K.—A. Habit (× ½). [After *Busey* 327 (MO).]—B. Glomerule (× 5). [After *Dwyer et al.* 4349 (MO).]—C. Head and bract (× 5).—D. Achene (× 10). [After *Lewis et al.* 5438 (MO).]

Ranging from British Honduras to Venezuela, in Panama *Spiracantha cornifolia* is mainly restricted to central Panama, often on thin soil. It flowers principally from December to April. The glomerules do not fall apart but are disseminated intact.

CANAL ZONE: Albrook Forest, *Blum & Dwyer 2093* (FSU, MO). France Field, *Blum & Dwyer 2120* (MO). Barro Colorado Island, *Busey 309* (FSU, MO). 10 km N of Gamboa, *Busey 327* (C, DUKE, ENCB, MO, OS, PMA, US, WIS). Near Albrook, *Correa 118* (DUKE, FSU). Barro Colorado Island, *Croat 7460, 7776, 8246, 11998* (all MO). Madden Forest, *Croat 8944* (MO). Pipeline Road 2.5 mi from Gamboa, *Croat 9341* (MO). 15 mi NW of Gamboa, *Croat 12771* (MO). Albrook, *Dwyer & Robyns 38* (MO). Arraiján, *Dwyer et al. 4349* (MO). Barro Colorado Island, *Ebinger 11* (DUKE, MO). 11 mi NE of Balboa, *Eyerdam 12064* (US). 5–10 mi N of Gamboa, *Gentry 2655* (MO). Ancón, *Greenman & Greenman 5049* (GH, MO). Pipeline Road, 5.9 mi from Gamboa turnoff, *Kennedy 2345* (MO). Near Gamboa, *Lazor & Tyson 5660* (MO). Madden Forest, *Lewis et al. 5310* (DUKE, MO, NY). Barro Colorado Island, *Luteyn 773* (DUKE). Between Rodman Marine Base and Chorrera, *Nowicke et al. 3595* (MO). Chiva-Chiva Trail near Pueblo Nuevo, *Piper 5760* (US). Summit, *Standley 26906* (US). Gatún Station, *Tyson 3519* (MO). Ft. Clayton, *Tyson 3659* (FSU, MO). 12 mi S of Colón, *Tyson et al. 4488* (FSU, MO). Pipeline Road N of Gamboa, *Wilbur & Weaver 11244* (DUKE, MO). 1 mi SW of Cocolí, *Wilbur et al. 12877* (DUKE, GH, MO). Playa Venado, *Wilbur & Teeri 12980* (DUKE). 6 mi NW of Gamboa, *Wilbur & Teeri 13356* (DUKE, GH, MO, NY). Near Summit, *Wilbur & Teeri 13383* (DUKE). COCLÉ: Río Grande, *Burch et al. 1178* (GH, MO, US). COLÓN: Between Transisthmian Hwy. and Salamanca, 100 m, *Gentry 6726* (MO). DARIÉN: Río Sabana, *Duke 15452* (OS). HERRERA: Between Chitré and Divisa, *Burch et al. 1365* (MO). PANAMÁ: Isla del Rey, *Duke 9574* (DUKE, MO, OS). Cerro Azul, *Dwyer 2410* (ENCB, MO). Near Cerro Jefe, *Dwyer 7138* (GH, MO). San José Island, *Johnston 170* (GH); *1199* (GH). Cerro Campana, *Lewis et al. 3117* (DUKE, MO). Ca. 16 mi N of Gamboa, *Lewis et al. 5438* (MO). Sabanas N of Panama City, *Paul 622* (US). Near Juan Franco Race Track, *Standley 27709* (US). Between Matías Hernández and Juan Díaz, *Standley 32043* (US). Cerro Campana, 2300 ft, *Tyson 4021* (FSU, MO). 4 mi E of Chepo, *Tyson 5354* (DUKE, FSU, MO). Near Goofy Lake, *Wilbur & Weaver 11107* (DUKE). Cerro Azul, *Wilbur & Teeri 13597* (DUKE).

II. EUPATORIEAE[7]

R. M. KING[8] AND H. ROBINSON[8]

Eupatorieae Cass., Jour. Phys. 88: 202. 1819. TYPE: *Eupatorium* L.

Herbs, vines, shrubs or small *trees*, terrestrial or epiphytic. *Leaves* opposite, alternate or whorled, simple or rarely compound, usually petiolate. *Heads* discoid with 1–ca. 300 florets; involucral bracts in 1–8 series, usually separate, commonly imbricated, herbaceous or coriaceous; receptacle flat to hemispherical or conical, glabrous or hairy, mostly without paleas; florets perfect and fertile, cells without raphids; corollas tubular to campanulate or funnelform, rarely irregular, white, blue, pink, red or purple, never yellow, lobes 5(4), glabrous to glanduliferous or hairy; stamens 4–5, the thecae rounded or hastate at base, never tailed, the exothecial cells usually quadrate with thickenings on both lateral and transverse walls, the appendage vestigial to elongate, flat and often hollow; style base with or without enlargement, glabrous to hirsute, immersed in nectary, the style branches well-developed, sometimes glanduliferous, the stigmatic surface of two

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distinct lines restricted to lower half of lateral margins, rarely on inner surface and reaching nearer tip, the appendages flattened to terete, papillose or smooth, filiform or clavate. *Achenes* prismatic or flattened, 2–10-ribbed (usually 5 or 10), setiferous or glanduliferous, the base usually forming a distinct symmetrical or asymmetrical carpopodium; pappus of scales, awns, bristles, or coroniform to completely lacking, in two genera forming glanduliferous knobs, persistent or deciduous, rarely in more than one series. *Pollen* spherical, usually ca. 18–25 μ in diameter, tricolporate, rarely almost smooth, usually short-spinose, never lophorate, with rather simple wall structure.

The tribe is very diversified with more than 100 genera and more than 2,000 species. Most of the genera and species are confined to the New World. The most commonly recognized distinguishing features of the tribe are the usually elongate sometimes expanded style appendages and the exclusively homogamous flowers in the heads. Leaves are mostly opposite.

The taxonomy of the Eupatorieae has been extensively revised at the generic level and some of the revisions are cited in the following text. The need for revision has been exceptionally great because the previously emphasized characters have proven particularly unreliable. The revisions have been aided by the use of distinctive microscopic floral characters (King & Robinson, 1970) which are particularly well-developed in the tribe.

As this treatment went to press, Williams (1975) presented a treatment of the Eupatorieae in Guatemala and adjacent regions differing from that presented here.

Literature:

King, R. M. & H. Robinson. 1969. Studies in the Compositae-Eupatorieae, XI. Typification of genera. Sida 3: 329–342.

——— & ———. 1970. *Eupatorium*, a composite genus of Arcto-tertiary distribution. Taxon 19: 769–774.

Williams, L. O. 1975. Tropical American plants, XVII. Fieldiana, Bot. 36: 77–110.

a. Heads with 3–5 involucral bracts and usually an equal number of florets.
  b. Anther appendages minute or lacking; anther filament with hairs or papillae; walls of achenes sparsely punctate internally (not visible without special techniques) ---------- 29. *Piqueria*
  bb. Anther appendages distinct, as long as wide or longer; anther filaments without hairs or papillae; walls of achenes densely minutely punctate internally.
    c. Plants scandent; heads with 4 florets and 4 principal involucral bracts; corollas glabrous inside, lobes smooth ---------- 27. *Mikania*
    cc. Plants erect herbs or subshrubs; heads with 5 florets and 5 equal involucral bracts; corollas with hairs inside, lobes papillose inside ---------- 31. *Stevia*
aa. Heads with more than 5 involucral bracts.
  d. Pappus lacking or of a few scales, knobs, or irregular projections.
    e. Pappus with 3–5 knobs bearing glands on tips.
      f. Anther appendages as long as wide or longer; style shaft glabrous; glands of pappus in discrete clusters on tips of knobs ---------- 30. *Sciadocephala*
      ff. Anther appendages not as long as wide; style shaft often with numerous hairs; glands of pappus in elongate clusters on tips and outer surfaces of knobs ---------- 10. *Adenostemma*
    ee. Pappus of scales, projections, or lacking, not bearing glands.

g. Receptacle not conical; shrubs epiphytic on mangroves ..... 32. *Tuberostylis*
gg. Receptacle conical; terrestrial herbs or subshrubs.
h. Paleas lacking; style branches filiform; style base not enlarged, glabrous ..... 12. *Ageratum*
hh. Paleas present; style branches short and tapering; style base distinctly enlarged, sometimes with hairs or papillae ..... 25. *Isocarpha*
dd. Pappus of 10 or more capillary bristles.
i. Involucral bracts not spreading when old or dry, all bracts deciduous leaving old receptacles completely bare ..... 17. *Chromolaena*
ii. At least outer involucral bracts spreading when old or dry, persistent.
j. Anther appendages shorter than wide.
k. Tips and base of style much enlarged; vines ..... 22. *Gongrostylus*
kk. Tips and base of style not or only gradually enlarged; not vines.
l. Receptacle glabrous; leaves opposite ..... 26. *Koanophyllon*
ll. Receptacle hairy; leaves alternate ..... 20. *Decachaeta*
jj. Anther appendages as long as wide or longer.
m. Style base with numerous hairs.
n. Achenes with 10 ribs, with many stiff hairs; pappus bristles flattened on outer surface, with pointed apical cells ..... 16. *Brickellia*
nn. Achenes with 5 ribs, with only glands; pappus bristles not flattened on outer surface, with blunt apical cells ..... 13. *Austroeupatorium*
mm. Style base glabrous.
o. Inner surface of corolla lobes mamillose or papillose with bulging cells, appearing granulose.
p. Involucre usually eximbricate with 2–3 series of subequal bracts; pappus often deciduous; corolla tube slender; corolla lobes usually longer than wide, smooth on outer surface ..... 11. *Ageratina*
pp. Involucre usually subimbricate with 3 or more series of distinctly unequal bracts; pappus not normally deciduous; corolla tube short and broad; corolla lobes not longer than wide, papillose on outer surface ..... 21. *Fleischmannia*
oo. Inner surface of corolla lobes smooth, without bulging cells.
q. Plants epiphytes or growing in deep humus; cells of corolla broad and quadrate ..... 28. *Neomirandea*
qq. Plants not epiphytes; cells of corolla narrow with sinuous walls.
r. Style base with distinct enlargement above the nectary; base of achene contorted or with prominent upper margin; inner bracts of involucre not noticeably deciduous.
s. Involucral bracts 15, in 5 ranks of 3; corolla with distinct campanulate limb ..... 18. *Condylidium*
ss. Involucral bracts not in 5 distinct ranks of 3; corolla narrowly funnelform.
t. Scandent shrubs; inflorescence with mostly thyrsoid branches; style branches with short papillae ..... 24. *Heterocondylus*
tt. Erect herbs; inflorescence with mostly cymose branches; style branches with long hairlike papillae ..... 14. *Ayapana*
rr. Style base not enlarged; base of achene not noticeably contorted and without prominent upper margin; inner bracts of involucre deciduous.
u. Heads usually with 4–12 florets; corolla usually glabrous; areoles of leaves with lacticifers ..... 19. *Critonia*
uu. Heads with 20–120 florets; corolla with few to many hairs or glands on outer surface; areoles of leaves without lacticifers.
v. Receptacle highly convex, composed of highly sclerified cells, central part easily broken off; style branches filiform ..... 23. *Hebeclinium*
vv. Receptacle slightly convex with parenchymatous core and sclerified surface; style branches narrowly linear to somewhat clavate ..... 15. *Bartlettina*

10. ADENOSTEMMA

Adenostemma J. R. & G. Forster. Char. Gen. Pl. 89. 1776. TYPE: *A. viscosa* J. R. & G. Forster.

Lavenia Swartz, Prodr. Veg. Ind. Occ. 112. 1788. TYPE: *L. erecta* Swartz.

Small to large perennial *herbs*, creeping or erect with usually procumbent bases, with few or no branches, with few to many glandular hairs on stems, leaves, and involucral bracts; stems usually fistulose. *Leaves* opposite with short to long petioles; blades narrowly elliptical to broadly ovate or hastate, the base slightly to strongly cuneate, trinervate, the apex acute to slightly acuminate. *Inflorescence* very laxly cymose, the branches elongate. *Heads* discoid with 10–60 florets; involucre of 10–30 mostly eximbricate bracts with often fused basal margins, in 2 slightly overlapping series, spreading when mature; receptacle convex, covered with discrete oval deeply concave scars, glabrous; corollas narrowly funnelform or with narrow tube and broadly campanulate limb, usually with hairs or glands on outer surface, hairs often moniliform, the lobes 4–5, nonpapillose, the cells of the limb fragile with thin straight or laxly sinuous walls; anther collars usually enlarged below, with few to many quadrate cells, the walls ornamented, the exothecial cells quadrate to very short, the anther appendage distinctly shorter than wide; style base glabrous, not enlarged, the style shaft usually with some hairs, the style appendages fleshy, rounded apically, usually broadly clavate, of smooth, thin-walled cells usually distorted when dry. *Achene* slightly curved, slightly 3–4-angled without distinct ribs; carpopodium forming a prominent somewhat asymmetrical knob with a stout vascular basal point, the cells subquadrate with firm thin walls; pappus of 3–4 terete clavate knobs (5 in Guatemalan species), the knobs with tips and upper outside surface covered with an elongate mass of viscid glands. *Pollen* with short spines.

Adenostemma is a genus of about 20 species occurring primarily at low elevations in Central America, the West Indies, South America, Asia, and Africa. An important characteristic of the genus is its achenes which have a sticky pappus allowing for easy distribution by animals. The genus seems to have the most successful distribution mechanism in the tribe since it occurs widely in Asia, Africa, and the Pacific where there are many distinct species.

Literature:

Grierson, A. J. C. 1972. Critical notes on the Compositae of Ceylon. Ceylon Jour. Sci., Biol. Sci. 10: 42–60.

King, R. M. & H. Robinson. 1974. Studies in the Eupatorieae (Asteraceae). CXXVII. Additions to the American and Pacific Adenostemmatinae. *Adenostemma*, *Gymnocoronis* and *Sciadocephala*. Phytologia 29: 1–20.

1. **Adenostemma platyphyllum** Cass., Dict. Sci. Nat. 25: 363. 1822. TYPE: Peru, *J. Jussieu*, perhaps Jussieu herb. no. 9119 as *Lavenia spathulatum* (P, not seen, US, microfiche).—FIG. 11.

Erect perennial *herb* up to 1 m tall, unbranched or branched at base; stems terete to weakly ribbed, glabrate. *Leaves* opposite; blades broadly ovate, up to

18 cm long and 13 cm wide, the base somewhat rounded and abruptly broadly decurrent on the petiole, strongly trinervate from near base with strongly ascending secondary veins remote from margin, the margin bluntly serrate or dentate to subentire, not angular, the apex bluntly short-acute or slightly acuminate, the surfaces with very few small hairs, the veins sparsely glandular-haired below; petioles up to 8 cm long, broadly winged above, the wings narrow or lacking in basal half. *Inflorescence* laxly and usually profusely cymosely branched, ultimate branches 1–3 cm long, usually densely glandular-puberulous. *Heads* 5–6 mm high and 5–7 mm wide with ca. 10–25 florets; involucral bracts ca. 10–20, eximbricate, in 2 series, oblong to slightly obovate, mostly 3–4 mm long, reaching only to the level of the corolla tubes, apically rounded with little or no scarious margin; corolla white often with a lavender limb, ca. 2.5 mm long, narrowly funnelform with a short tube and rather cylindrical limb, few to many glands on outer surface, the hairs restricted to near bases of the lobes, the lobes 5; anther collars broad below with many subquadrate cells; style shaft with many hairs, the style branches becoming exserted ca. 2 mm, very broadly clavate. *Achenes* 2.0–2.5 mm long, covered with glanduliferous tubercles; carpopodium prominently oblique toward inner side, fitting into deep, inwardly directed pits of receptacle; pappus usually of 3 glutiniferous knobs. *Pollen* 18–20 μ in diameter.

Adenostemma platyphyllum Cass. is distributed widely at lower elevations in South America from northernmost Argentina through Bolivia to southern Peru. To the north the species occurs in the coastal lowlands of Ecuador, Colombia, Panama, and Venezuela. The species is most distinct in its nonangular leaf margins, its very broad style branches, its longer corolla limb, and its short involucre. Close relatives include *A. berteri* DC. of the Greater Antilles with its more pointed involucral bracts and slightly sharper leaf tips. These and many other species in the genus have been identified with *A. lavenia* (L.) O. Kuntze of Ceylon, but the latter species has been interpreted much too broadly.

DARIÉN: Without precise locality, *Duke & Bristan s.n. 1966* (MO). PANAMÁ: Without precise locality, "On road-sides" *Seemann 1026* (BM, not seen; US, photo).

11. AGERATINA

Ageratina Spach, Hist. Veg. Phan. 10: 286. 1841. TYPE: *Eupatorium aromaticum* L.

Batschia Moench, Meth. 567. 1794, not *Batschia* Gmelin, 1791 (Boraginaceae); nor *Batschia* Mutis ex Thunb., 1792 (Menispermaceae); nor *Batschia* Vahl, 1794 (Leguminosae). TYPE: *B. nivea* Moench = *Eupatorium ageratoides* L.f.

Ageratiopsis Schultz-Bip. ex Benth. & Hook., Gen. Pl. 2: 246. 1873, nom. nud. TYPE: *Eupatorium ageratoides* L.f.

Mallinoa Coult., Bot. Gaz. (Crawfordsville) 20: 47. 1895. TYPE: *M. corymbosa* Coult.

Kyrstenia Neck. ex E. L. Greene, Leafl. Bot. Observ. Crit. 1: 8. 1903. TYPE: *Eupatorium aromaticum* L.

Sparingly to densely branched perennial *herbs* or *shrubs*. *Leaves* usually opposite, rarely subopposite or alternate, short- to long-petiolate; blade deltoid to narrowly elliptical, toothed or lobed to entire, serrate in most species. *Inflores-*

FIGURE 11. *Adenostemma platyphyllum* Cass.—A. Habit (× 2/5).—B. Head (× 5).—C. Style (× 11).—D. Achene (× 11).

cence laxly to densely corymbose. *Heads* discoid with 10–60 florets; involucre of ca. 30 rather narrow usually acute subimbricate bracts in 2–3 series, spreading at maturity; receptacle glabrous or with minute scattered hairs, usually slightly convex; corolla with a broad to very narrow basal tube and a narrowly to broadly campanulate limb, the lobes 5, slightly to distinctly longer than wide, densely

papillose on the inner surface, smooth with glands or hairs on the outer surface, the cells of the limb mostly narrow with sinuous walls; anther collars mostly narrow, with many quadrate cells below, elongate cells above, the walls with little or no ornate thickening, the exothecial cells in the outer valve usually longer than wide, the anther appendage large, longer than wide; style usually with distinct basal enlargement, glabrous, the style appendages usually densely long-papillose. *Achenes* prismatic or often fusiform, usually 5-ribbed, usually with bristles or glands or both; carpopodium distinct without a distinct upper rim, short- to long-cylindrical, the cells moderately large quadrate to oblong in many series with thin and beaded walls; pappus of 5–40 slender scabrous usually easily deciduous bristles, the zone of basal cells often fragile, the apices often enlarged, the apical cells acute. *Pollen* with short spines, often deformed and nonfunctional.

Ageratina is a large genus of approximately 230 species ranging from the eastern United States to Mexico, Central America, the West Indies, and western South America. Two species, *A. adenophora* (Spreng.) R. M. King & H. Robinson and *A. riparia* (Regel) R. M. King & H. Robinson, have become widely adventive in warmer parts of the Old World. Seven species have been collected in Panama.

Ageratina and a number of related genera such as *Oxylobus* form a distinct element in the tribe that is cytologically notable for its base numbers of $x = 17$ and $x = 16$ (King & Robinson, 1970, 1972).

Literature:

King, R. M. & H. Robinson. 1970. Studies in the Eupatorieae (Compositae). XIX. New combinations in *Ageratina*. Phytologia 19: 208–229.

——— & ———. 1972. Studies in the Eupatorieae (Asteraceae). LXXXV. Additions to the genus *Ageratina* with a key to the Costa Rican species. Phytologia 24: 79–104.

——— & ———. 1974. Studies in the Eupatorieae (Asteraceae). CXXVIII. Four additions to the genus *Ageratina* from Mexico and Central America. Phytologia 28: 494–502.

a. Corolla with short-stalked glands on outer surface, without hairs; involucral bracts without distinct striations; pappus spreading with age, not fragile at base ---------- 1. *A. anisochroma*

aa. Corolla without distinct glands on outer surface, with few to many hairs; involucral bracts bicostate; pappus fragile at base and easily deciduous.

b. Involucral bracts with glands on outer surface, with few or no hairs.

c. Leaves subsessile, petioles ca. 1 mm long; involucral bracts obtuse to sharply acute ---------- 3. *A. chiriquensis*

cc. Leaves distinctly petiolate, petioles mostly 1–4 cm long; involucral bracts with attenuate tips ---------- 5. *A. ixiocladon*

bb. Involucral bracts without glands on outer surface, with many hairs.

d. Leaves with narrowly acuminate tips; heads with 10–15 florets ---------- 4. *A. croatii*

dd. Leaves with tips obtuse to acute, not or scarcely acuminate; heads with 19–55 florets.

e. Leaves membranaceous; corolla tube distinctly longer than limb; inflorescence not densely branched ---------- 6. *A. molinae*

ee. Leaves papyraceous; corolla tube about as long as limb or shorter; inflorescence compactly corymbosely branched.

f. Leaf blades with cuneate bases, lower surface sparsely puberulous; heads with 19–28 florets; involucral bracts with only narrow scarious margins ..... 7. *A. whitei*

ff. Leaf blades with rounded to slightly cordate bases, lower surface often densely hirtellous; heads with 25–55 florets; inner involucral bracts with broad scarious margins ..... 2. *A. aschenborniana*

1. **Ageratina anisochroma** (Klatt) R. M. King & H. Robinson, Phytologia 19: 218. 1970.—Fig. 12.

Eupatorium anisochromum Klatt, Bull. Soc. Roy. Bot. Belgique 31: 186. 1892 (1893). TYPE: Costa Rica, environs de la laguna du Barba, *Pittier 1940* (GH, not seen).

E. durandii Klatt, Bull. Soc. Roy. Bot. Belgique 31: 189. 1892 (1893). TYPE: Costa Rica, Poás, *Pittier 387* (GH, not seen).

E. adspersum Klatt, Leopoldina Bot. Beibl. 1895: 1. 1895. TYPE: Costa Rica, bridge of Cariblanco road to Sarapiquí, *Biolley 7422* (GH?, not seen).

E. polanthum Klatt, Leopoldina Bot. Beibl. 1895: 3. 1895. TYPE: Costa Rica, cuesta de Tarrazú, *Tonduz 7797* (BR, holotype; US, isotype).

Subshrub or *shrub* to 2 m tall, with few to many branches; stems yellowish with small red maculae, becoming brown below, terete, sparsely to densely hirtellous. *Leaves* opposite; blades ovate to narrowly lanceolate, subcoriaceous, up to 11 cm long and 4 cm wide, in some forms mostly 2 cm long, the base narrowly cuneate, the margins closely to rather remotely serrate, the apex narrowly acute to slightly acuminate, in small forms shortly acute, the upper surface usually dark green, glabrous, the lower surface very pale, smooth with scattered glandular punctations, 2–3 pairs of strongly ascending secondary veins in basal third or fourth; petioles very short to scarcely distinct, 1–5 mm long. *Inflorescence* broadly corymbose-paniculate with corymbose branches, the ultimate branches 1–5 mm long, densely puberulous. *Heads* 4–5 mm high with ca. 17 florets; involucral bracts ca. 10, eximbricate, biseriate, broadly oblong to ovate, 2.5–3.0 mm long, mostly 1 mm wide, not costate, obtuse to short-acute, the outer surface puberulous with small scattered glandular punctations; corolla white or lavender, ca. 2.3 mm long, the tube slender, ca. 1 mm long, with glands and often with numerous short stiff biseriate hairs, the limb broadly funnelform, the lobes as long as the limb, triangular, 1½ times as long as wide, only low papillae on inner surface and only glands on outer surface; anther thecae ca. 0.5 mm long, with truncate to short-hastate bases; style base slightly enlarged, the style appendages strongly papillose. *Achenes* broadly prismatic, ca. 1 mm long, with short bristles on ribs; carpopodium short-cylindrical to rounded, with subquadrate cells; pappus bristles ca. 25, persistent and spreading at maturity, mostly ca. 2.2 mm long, with very slender tips, without distinct series of shorter bristles.

Ageratina anisochroma is known only from Nicaragua, Costa Rica, and western Panama. The species is named after the distinctive difference in color of the upper and lower surfaces of the leaves. The species is also distinct in the structure of the involucral bracts, the shape of the corolla, the less strongly papillose corolla lobes, and the nondeciduous nature of the pappus.

CHIRIQUÍ: 8 mi NE of El Volcán, 8100–8400 ft, *Tyson 844* (FSU, MO). W slope of El Barú, 7000–8000 ft, *Tyson & Loftin 5996* (MO, US). Valley of the upper Río Chiriquí Viejo, *White 59* (MO).

FIGURE 12. *Ageratina anisochroma* (Klatt) R. M. King & H. Robinson.—A. Habit (× ½).—B. Head (× 4⅗).—C. Floret with achene (× 16).—D. Style (× 14).

2. **Ageratina aschenborniana** (Schauer) R. M. King & H. Robinson, Phytologia 19: 212. 1970.

Eupatorium aschenbornianum Schauer, Linnaea 19: 720. 1847. TYPE: Mexico in valle Toluccana, *Aschenborn 106* (B, destroyed, US, photo).

E. vulcanicum Benth. ex Örsted, Vidensk. Meddel. Dansk Naturhist. Foren. Kjøbenhavn 78. 1852. TYPE: Costa Rica, Irasú, *Örsted 56* (C).

E. donnell-smithii Coult., Bot. Gaz. (Crawfordsville) 16: 95. 1891. TYPE: Guatemala, Aceituna, *Donnell Smith 2374* (US).
Kyrstenia donnell-smithii (Coult.) E. L. Greene, Leafl. Bot. Observ. Crit. 1: 9. 1903.
Ageratina vulcanica (Benth. ex Örsted) R. M. King & H. Robinson. Phytologia 19: 218. 1970.

Shrub to 1.5 m tall, with few to many branches; stems pale to dark brown, terete, sparsely to densely hirsute. *Leaves* opposite; blades broadly ovate, to 10 cm long and 6 cm wide, the base usually slightly cordate to broadly rounded, rarely slightly cuneate, the margins crenulate-serrate to crenate, the apex broadly acute to short-acuminate, the upper surface minutely puberulous, more so on the veins, the lower surface densely puberulous to hirtellous, often densely hirsute on veins, the veins trinervate from at or near base; petioles slender, to 3.5 cm long. *Inflorescence* corymbose-paniculate with corymbose branches, the ultimate branches mostly 1–5 mm long, rarely to 12 mm, densely puberulous or hirtellous. *Heads* 5–6 mm high with 25–55 florets; involucral bracts 17–20, eximbricate, biseriate, narrowly oblong to linear, 3.0–4.5 mm long, bicostate, the apices obtuse to sharply acute, the scarious margins of inner bracts very broad, the outer surface puberulous to prominently pilose; corolla white, 2.5–4.0 mm long, the tube slender, 1.0–2.0 mm long, glabrous, the limb cylindrical to narrowly campanulate, the lobes triangular, 0.3–0.4 mm long, without hairs inside and with few to many hairs on outer surface; anther thecae ca. 0.7 mm long. *Achenes* fusiform, 1.5–1.8 mm long with many bristles mostly on the ribs; carpopodium cylindrical with mostly oblong cells; pappus bristles ca. 20, fragile at base, mostly 3.0–3.5 mm long, scarcely to distinctly broadened distally, with few or no distinct shorter bristles.

Ageratina aschenborniana is common from central Mexico southward through Central America to western Panama. The species is rather distinct in the rounded to cordate bases of the leaf blades and in the often very large number of flowers in the heads. *Ageratina vulcanica* has been regarded as a distinct species, but more careful analysis shows an erroneously low flower number cited for *A. vulcanica* and a slightly greater range of flower number in *A. aschenborniana*. There is some variation in the material from Panama, Costa Rica, and Nicaragua with some specimens having more hirsute involucral bracts, larger corollas, and more broadly tipped pappus bristles. The differences do not seem entirely correlated, however, and the variants are not worthy of taxonomic status.

CHIRIQUÍ: Vic. of "New Switzerland" central valley of Río Chiriquí Viejo, *Allen 1371* (F, MO). Trail from Paso Ancho to Monte Lirio, upper valley of Río Chiriquí Viejo, 1500–2000 m, *Allen 1580* (F, MO). Cerro Copete, E spur of Chiriquí Volcano, 8000–8500 ft, *Allen 4865* (MO). On way to Lerida, Volcán de Chiriquí, 4400 ft, *Maurice 870* (US). Vic. of Bambito, *Croat 10623* (MO). 1 mi N of El Hato del Volcán, *Croat 10694* (MO). Forested hill N of Audubon Cabin, *Croat 13626* (MO). Vic. of Las Nubes, 2.7 mi NW of Río Chiriquí Viejo, W of Cerro Punta, 2200 m, *Croat 22355* (MO). Along Río Chiriquí Viejo, just above Guadelupe, *Croat & Porter 16030* (MO). Slope of Cerro Respinga above town of Cerro Punta, 8400 ft, *D'Arcy & D'Arcy 6548* (MO). Boquete, Bajo Chorro, 6000 ft, *Davidson 154* (F, MO, US). Boquete, Volcán de Chiriquí, 8000 ft, *Davidson 940A* (GH, MO). Ca. 1 mi W of Cerro Punta, 1740 m, *McDaniel 10025* (FSU). Nueva Suiza, *Partch 69-10* (MO). Pastures around El Boquete, 1000–1300 m, *Pittier 2859, 2900* (both US). Vic. of Cerro Punta, 6800 ft, *Ridgway & Solis 2402* (MO). Valley of the upper Río Chiriquí Viejo, vic. of Monte Lirio, 1300–1900 m, *Seibert 134* (MO, US). Cerro Punta, ca. 2150 m, *Tyson 1024* (FSU, US). W slope of El Barú, 6000–7000 ft, *Tyson & Loftin 5951* (MO, US). Vic. of Finca Lérida, 1750 m, *Woodson & Schery 211* (US). Potrero Muleto to summit, Volcán de Chiriquí, 3500–4000 m, *Woodson &*

Schery 462 (MO). Vic. of Casita Alta, Volcán de Chiriquí, ca. 1500–2000 m, *Woodson et al. 861* (MO, US).

3. **Ageratina chiriquensis** (B. L. Robinson) R. M. King & H. Robinson, Phytologia 19: 213. 1970.

Eupatorium chiriquense B. L. Robinson, Proc. Amer. Acad. Arts 54: 238. 1918. TYPE: Panama, Chiriquí Volcano, *Maxon 5360* (US).

Small *shrub* to 0.5 m tall, with many branches; stems pale to dark brownish, terete, puberulous, the internodes usually short. *Leaves* opposite; blades narrowly ovate, papyraceous, to 2–3 mm long and 1.4 mm wide, the base rounded, the margins serrate, the apex acute, the upper surface glabrous, the lower surface slightly paler, sparsely puberulous on veins, the veins somewhat trinervate from near the base; petioles mostly 1–2 mm long. *Inflorescence* corymbose, the ultimate branches 3–7 mm long, usually densely stipitate-glandular. *Heads* 5–7 mm high with ca. 26 florets; involucral bracts ca. 20, eximbricate, biseriate, narrowly oblong to linear, mostly 3.5–5.5 mm long, bicostate, the apices obtuse to sharply acute, the outer surface with scattered short- to long-stipitate glands; corolla white to pale lavender, 4.0–4.5 mm long, the tube slender, 1.5–2.0 mm long, glabrous, the limb cylindrical to narrowly campanulate, the lobes short-triangular, 0.5–0.7 mm long, glabrous on inner surface and with few to many hairs on outer surface; anther thecae ca. 1 mm long. *Achenes* fusiform, 1.7–2.0 mm long, with few to many short bristles mostly on the ribs; carpopodium cylindrical with mostly oblong cells; pappus bristles ca. 20, rather fragile at base, mostly 3.5–4.0 mm long, slightly broadened distally, often with partial series of much shorter bristles.

Ageratina chiriquensis is endemic to the region of Chiriquí. The nearly sessile leaves distinguish the species from all other species of *Ageratina* in the area, including the closely related *A. ixiocladon*.

CHIRIQUÍ: Summit of Chiriquí Volcano, 3600 m, *Killip 3599* (US); 3374 m, *Maxon 5360* (US). Side of Barú Mtn., 2900 m, *McCorkle c-153* (FSU). Upper belt of Chiriquí Volcano, N slope, 3000–3374 m, *Pittier 3089* (US), El Barú, above 11000 ft, *Tyson & Loftin 6157* (MO, US), *6177* (FSU, MO). Volcán de Chiriquí, *Sapper s.n.* (US); ca. 2500–3380 m, *Woodson et al. 1077* (MO, US), *1083* (MO).

4. **Ageratina croatii** R. M. King & H. Robinson, Phytologia 29: 347. 1975. TYPE: Panama, Chiriquí, *Croat 26432* (US).

Coarse *herbs* or *subshrubs* to 1 m high, with few branches; stems yellowish-brown, terete, somewhat densely puberulous above. *Leaves* opposite; blades papyraceous, ovate, mostly 5–8 cm long and 1.5–4.0 cm wide, the base short-cuneate to rounded, trinervate, the margins closely doubly serrate, the apex narrowly acuminate, the upper and lower surfaces with puberulence mostly on the veins, the secondary veins few, strongly ascending; petioles slender, 10–25 mm long. *Inflorescence* somewhat lax, broadly corymbose-paniculate, the ultimate branches 1.5–5.0 mm long, densely puberulous. *Heads* ca. 4 mm high with 10–15 florets; involucral bracts ca. 15, eximbricate, in 2 series, linear-lanceolate, 3.5–4.0 mm long and 0.4–0.5 mm wide, bicostate, the tips short-acute with a short fringe of marginal hairs, nonscarious, the lateral margins narrowly scarious, the outer surface sparsely puberulous; corolla white?, ca. 2.3 mm long, the tube narrow, ca.

1 mm long, with few hairs, the limb narrowly funnelform, with few hairs, the lobes short-triangular, ca. 0.3 mm long and wide, glabrous on inner surface and with numerous hairs on outer surface, without glands; anther thecae ca. 0.5 mm long. *Achenes* fusiform, ca. 1.3 mm long, with many short bristles on the ribs, without glands; carpopodium cylindrical, ca. 0.1 mm long, on a slender stipe, the cells mostly narrowly oblong; pappus of ca. 20 slender fragile scabrous bristles, mostly 2.5 mm long, the tips scarcely broader, the apical cells minutely apiculate, distinct series of very short bristles present.

The species is known only from the type collection. *Ageratina croatii* is distinct among the related group of species in Panama by the narrowly acuminate leaves, by the reduced number of florets in the head, and by the short lobes of the corolla. Closest relationship may be to *A. costaricensis* R. M. King & H. Robinson which also has a lax inflorescence and trinervate leaves. The latter species, however, has less acuminate leaves, larger heads, and longer corolla lobes.

CHIRIQUÍ: Las Nubes near Cerro Punta, ca. 2000 m, *Croat 26432* (US).

5. **Ageratina ixiocladon** (Benth. in Örsted) R. M. King & H. Robinson, Phytologia 19: 223. 1970.

Eupatorium ixiocladon Benth. in Örsted, Vidensk. Meddel. Dansk Naturhist. Foren. Kjøbenhavn 77. 1852. TYPE: Costa Rica, Irazú, *Örsted 51* (C).

Subshrub or *shrub* to 3.6 m tall, with few to many branches; stems pale to dark brownish, terete, usually puberulous, sometimes glanduliferous. *Leaves* opposite; blades ovate, papyraceous, to 12 cm long and 6 cm wide, the base rounded to cuneate, the margins serrulate to crenate, the apex slightly to slenderly acuminate, the surfaces minutely puberulous on the veins, the lower surface slightly paler with rather prominent dark fine reticulations and scattered glandular punctations or short stipitate glands, usually 2 pairs of strongly ascending secondary veins from near base; petioles slender, mostly 1–4 cm long. *Inflorescence* broadly corymbose-paniculate with corymbose branches, the ultimate branches mostly 2–5 mm long, minutely puberulous. *Heads* 4–6 mm high with 19–30 florets; involucral bracts ca. 20, eximbricate, biseriate, linear to linear-lanceolate, 3.5–5.5 mm long, bicostate, the apices long attenuate, the outer surface with scattered glands and few or no hairs; corolla white to lavender, 2.5–3.5 mm long, the tube slender, 1.0–1.5 mm long, glabrous, the limb cylindrical to narrowly campanulate, the lobes triangular, 0.3–0.4 mm long, with few or no hairs on inner surface and numerous hairs on outer surface; anther thecae 0.4–0.9 mm long. *Achenes* fusiform, ca. 2 mm long, with short to long bristles mostly on the ribs; carpopodium cylindrical with mostly oblong cells; pappus bristles ca. 25, somewhat fragile at base, mostly 3.5–4.0 mm long, broadened distally, without distinct series of shorter bristles.

Ageratina ixiocladon is known only from Costa Rica and adjacent western Panama. The name has at various times been applied to material of a number of species in at least three eupatorian genera. The present concept is based on observation of the type material. The species is one of a closely related series having glands rather than hairs on the involucral bracts.

CHIRIQUÍ: Slopes of Las Cumbres, near Cerro Punta, *Croat 13728* (MO). Boquete, Bajo Chorro, 6000 ft, *Davidson 138* (MO). Volcán de Chiriquí, 8000 ft, *Davidson 940* (F, US); 11200 ft, *Terry 1319* (F). W slope of El Barú, 8000–9000 ft, *Tyson & Loftin 6116* (MO), *6116B* (US).

6. **Ageratina molinae** R. M. King & H. Robinson, Phytologia 24: 93. 1972. TYPE: Honduras, cloud forest above San Juancito, Morazán, *Williams & Molina 13767* (US).

Small erect or decumbent *shrubs* to 1 m high, with few to many branches; stems yellowish to purple-tinged, terete, puberulous. *Leaves* opposite; blades membranaceous, ovate to rhomboid, to 4.5 cm long and 3.5 cm wide, the base very short-cuneate to subtruncate, trinervate, the margins serrate to subentire, the apex short-acuminate, the surface sparsely short puberulous, the veins hirtellous; petioles slender, 0.5–3.0 cm long. *Inflorescence* laxly corymbose-paniculate with laxly corymbose branches, the ultimate branches slender, 2–9 mm long, puberulous. *Heads* ca. 5 mm high with 19–28 florets; involucral bracts 16–18, eximbricate, biseriate, narrowly lanceolate, 3.5–4.0 mm long, bicostate, mostly long acute, scarcely attenuate, the outer surface puberulous, without glands; corolla white, 3.0–3.5 mm long, the tube very slender, 1.5–2.0 mm long, glabrous, the limb short campanulate, ca. 1.0 long, the lobes triangular, scarcely longer than wide, glabrous on inner surface and with numerous simple hairs on outer surface; anther thecae ca. 0.5 mm long. *Achenes* fusiform, ca. 1 mm long, with scattered long bristles on the ribs and surface; carpopodium cylindrical with narrowly oblong cells; pappus bristles ca. 25, somewhat fragile at base, mostly 1.7–2.0 mm long, not distinctly broadened distally, shorter series of bristles lacking.

The species is distributed through southern Central America from El Salvador and Honduras to Costa Rica and western Panama. The most distinctive character of the species is the very small limb of the corolla which is shorter than the tube. The plants have a resemblance to *Fleischmannia microstemon* in their membranaceous somewhat rhomboid leaves and their moderately lax inflorescences, but differ in the eximbricate involucre and long narrow corolla tube.

CHIRIQUÍ: Llanos del Volcán, ca. 1300 m, *Allen 1543* (F, MO, US).

7. **Ageratina whitei** R. M. King & H. Robinson, Phytologia 28: 496. 1974. TYPE: Panama, Chiriquí, *White & White 118* (MO).

Shrubs to 1.7 m high, with few to many branches; stems brownish, terete to slightly hexagonal, sparsely minutely puberulous. *Leaves* opposite; blades subcoriaceous, narrowly ovate, mostly 3–5 cm long and 1.0–2.5 cm wide, the base cuneate or sometimes slightly acuminate, the margins closely crenate-serrate, the apex slightly acuminate, sharp, the upper and lower surfaces sparsely minutely puberulous, the veins more densely appressed-puberulous, the secondary veins few, pinnate; petioles slender, 3–7 mm long. *Inflorescence* a lax broad corymbose-panicle with densely corymbose branches, the ultimate branches 1–6 mm long, appressed-puberulous. *Heads* ca. 5 mm high with 25–29 florets; involucral bracts ca. 20, eximbricate to slightly subimbricate, in ca. 3 series, lanceolate to linear,

1.5–4.0 mm long and 0.5–0.7 mm wide, bicostate, sharply acute, without distinct scarious margins above, the outer surface sparsely appressed-puberulous, without glands; corolla pink, 3.5–4.0 mm long, the tube narrow, 1.0–1.5 mm long, the limb narrowly campanulate, with few hairs on outer surface, the lobes narrowly triangular, ca. 0.6–0.7 mm long, with many simple hairs on outer surface, without glands, glabrous on inner surface; anther thecae 0.8 mm long. *Achenes* fusiform, ca. 1 mm long, scabrid with mostly short bristles on the ribs and without glands; carpopodium cylindrical, 0.2–0.3 mm long, the cells mostly narrowly oblong; pappus of ca. 25 slender fragile densely scabrous bristles, mostly 3.0–3.5 mm long, the tips not broadened, the apical cells sharply acute, without distinct series of shorter bristles.

Ageratina whitei is known only from the type collection. The species seems most closely related to *A. tonduzii* (Klatt) R. M. King & H. Robinson of Costa Rica which has similar narrowly cuneate pinnately veined leaves, elongate cylindrical carpopodia, puberulous involucral bracts, 25–29 florets per head, and pink corollas. The Costa Rican species is most distinct in the much longer narrowly elliptical leaves up to 10 cm long. The leaves of *A. whitei* are similar to those of *A. ixiocladon* but that species has glands rather than hairs on the involucral bracts and usually has a few hairs on the inner bases of the corolla lobes.

CHIRIQUÍ: Valley of the upper Río Chiriquí Viejo, *White & White 118* (MO).

12. AGERATUM

Ageratum L., Sp. Pl. 2: 839. 1753. TYPE: *A. conyzoides* L.

Carelia G. Pontedera ex P. C. Fabricius, Enum. 85. 1759. TYPE: *A. conyzoides* L.

Annual *herbs* to perennial *subshrubs*, with few to many branches, the base often decumbent with numerous adventitious roots. *Leaves* opposite or alternate, petiolate; blades elliptical or lanceolate to deltoid or ovate, the margins entire to dentate or shallowly lobed, the undersurface usually with obvious sessile or sunken glandular-punctations, usually trinervate from the base. *Inflorescence* cymose to subcorymbose, sometimes subumbellate. *Heads* discoid with 20–125 florets; involucral bracts 30–40, eximbricate, equal or subequal, in 2–3 series, lanceolate, coriaceous; receptacle conical, glabrous or paleaceous; corolla funnelform or with distinct basal tube, the lobes 5, about as long as wide, papillose on inner surface, sometimes hispidulous on outer surface, the cells of the limb elongate with sinuous walls; anther collars slender, the walls of the cells with distinct annular thickenings, the anther appendage large, longer than wide; style base without enlarged node, glabrous, the style appendages linear, usually strongly and densely papillose. *Achenes* 4–5-ribbed, glabrous or with short bristles on the ribs; carpopodium distinct, large, usually asymmetrical; pappus lacking or coroniform or of 5–6 free flattened sometimes awn-like scales. *Pollen* with short spines.

The genus *Ageratum* contains 43 species and ranges from Mexico and Central America to the West Indies and South America. Two species, *A. conyzoides* and *A. houstonianum*, are widely adventive in warmer parts of the Old World. Six species have been collected in Panama.

Literature:

Grierson, A. J. C. 1972. Critical notes on the Compositae of Ceylon. Ceylon Jour. Sci., Biol. Sci. 10: 42–60.

Johnson, M. F. 1971. A monograph of the genus *Ageratum* L. (Compositae-Eupatorieae). Ann. Missouri Bot. Gard. 58: 6–88.

King, R. M. & H. Robinson. 1972. Studies in the Eupatorieae (Asteraceae). LXXXVII. Additions to the genus, *Ageratum*. Phytologia 24: 112–117.

Robinson, B. L. 1913. II. Revisions of *Alomia*, *Ageratum* and *Oxylobus*. Contr. Gray Herb. 42: 438–491.

a. Stems puberulous to hirtellous with short hairs, often becoming glabrous; petioles usually 2–5 mm long.
   b. Leaf blades narrowly elliptical to narrowly lanceolate, with narrowly cuneate bases ---------- 1. *A. chiriquense*
   bb. Leaf blades ovate to ovate-lanceolate, with rounded to shortly cuneate bases ---------- 6. *A. panamense*

aa. Stems sparsely to densely pilose with long hairs; petioles usually 10–30 mm long.
   c. Involucral bracts without scarious or irregular margins, glabrous; achenes glabrous ---------- 5. *A. oliveri*
   cc. Involucral bracts with scarious and often toothed margins, with few to many hairs on outer surface; achenes often scabrid or with short bristles on the ribs.
      d. Pappus lacking ---------- 4. *A. microcarpum*
      dd. Pappus of larger scales or awns.
         e. Corolla less than 2 mm long, not as long as the awned pappus scales; style branches very slender with papillae forming nearly ½ the width ---------- 2. *A. conyzoides*
         ee. Corolla over 2 mm long, as long as or longer than the awned pappus scales; style branches slightly broader distally, with small pointed papillae forming less than ¼ the width ---------- 3. *A. houstonianum*

1. **Ageratum chiriquense** (B. L. Robinson) R. M. King & H. Robinson, Phytologia 24: 113. 1972.

Alomia chiriquensis B. L. Robinson, Contr. Gray Herb. 61: 4. 1920. TYPE: Panama, between Cerro Vaca and Hato del Loro, Chiriquí, *Pittier* 5389 (US).

Erect perennial *herbs* or *subshrubs* to 0.6 m tall; stems purplish, terete, slightly striate, solid to slightly fistulose, obscurely puberulous, becoming glabrous. *Leaves* mostly opposite or ternate; blades narrowly elliptical or narrowly lanceolate, to 9 cm long and 1.7 cm wide, the base narrowly cuneate, the margins subentire to somewhat remotely serrate in the distal half, the apex usually narrowly acute to slightly acuminate, sometimes short acute, the upper surface dark green, shiny with elongated areolae, bullate, scabrid with many scattered hairs, the lower surface pale and fleshy with immersed glandular-punctations, densely short-pilose on the veins; petioles indistinct, usually 5 mm long. *Inflorescence* with few or no long branches, ending in rather compact corymbose to subumbellate clusters, branches densely puberulous, the ultimate branches mostly 2–9 mm long, not noticeably enlarged above. *Heads* ca. 6 mm high with mostly 50–100 florets; involucral bracts 20–25, eximbricate, in 2 series, mostly 3–4 mm long, oblong-lanceolate to linear-lanceolate, bicostate, without evident scarious margins, the apex somewhat callose, narrowly acute, the outer surface rather densely hirtellous, with prominent glandular-punctations; receptacle naked; corolla and style branches bluish; corolla 3.0–3.5 mm long, narrowly funnelform, with scattered

distinct capitate glands on outer surface of tube, limb and lobes, the tube somewhat broad and indistinct, the lobes ca. 0.5 mm long, with papillae only on the inner surface; style branches slightly broader distally, prominent, with minute papillae. *Achenes* ca. 1.2–1.5 mm long, glabrous; carpopodium asymmetrical; pappus lacking or of a few vestigial broad lobes.

The species is apparently endemic to the Chiriquí region of Panama. It is most distinct among the Panamanian members of the genus by the very narrowly cuneate short-petiolate bases of the leaves. The superficially similar *A. benjamin-lincolnii* R. M. King & H. Robinson (*Alomia guatemalensis* B. L. Robinson) of Guatemala differs most obviously by the presence of paleas on the receptacle.

CHIRIQUÍ: Boquete Lookout, 4000 ft, *D'Arcy & D'Arcy 6323* (MO). Lava fields near the town of Volcán, ca. 4600 ft, *Duke 9139* (MO). Between El Hato (Volcán) and Cerro Punta, *Ebinger 796* (MO, US). Between Cerro Vaca and Hato del Loro, 850–1100 m, *Pittier 5389* (US). Llanos Francia, 3300 ft, *Stern et al. 1174* (MO).

2. **Ageratum conyzoides** L., Sp. Pl. 2: 839. 1753. TYPE: America (Herb. Linn. 979.1 or 979.2, not seen, US, microfiche).

A. hirtum Lam., Encycl. Méth. 1: 54. 1783. TYPE: Cape of Good Hope, *Sonnerat* (P, not seen, US, microfiche).
A. humile Salisb., Prodr. Stirp. 188. 1796. TYPE: England, Chapel Allerton, *Salisbury*? (K?, BM?, not seen).
A. hirsutum Lam. in Poiret, Encycl. Méth. Bot. Suppl. 1: 242. 1810. TYPE: *Lamarck*, Illust. *tab. 672, fig. 2.*
A. album Willd. ex Steud., Nom. Bot., ed. 1. 18. 1821, nom. nud.
Cacalia mentrasto Vell., Fl. Flum. 339. 1825. TYPE: Vellozo, Fl. Flum. 8, *tab. 69.* 1831. Vellozo types at the "Cabinet d'Histoire naturelle de Rio de Janeiro" not known to exist.
Ageratum cordifolium Roxb., Fl. Ind. 3: 415. 1832. TYPE: India, Bengal, perhaps Wallich Cat. 3177/287 (K, not seen; G, not seen, US, microfiche).

Annual or short-lived perennial erect *herbs* or *subshrubs* to 1.5 m tall, sparingly branched; stems becoming brownish to slightly reddish, terete, slightly striate, usually fistulose, sparsely to densely long-pilose, usually also slightly puberulous. *Leaves* mostly opposite; blades ovate to broadly ovate, to 10 cm long and 7 cm wide, the base rounded to cuneate, strongly trinervate from the base, the margins usually crenate, the apex short-acute to narrowly rounded or obtuse, the upper surface dull green, sparsely long-pilose, the lower surface slightly paler green, prominently glandular-punctate, sparsely pilose on the veins and veinlets; petioles to 2.5 mm long. *Inflorescence* cymose to subcymose with compact corymbose to subumbellate branches, the branches somewhat densely puberulous with few to many longer hairs, the ultimate branches 3–10 mm long, often slightly enlarged distally. *Heads* ca. 4.0–4.5 mm high with ca. 50 florets; involucral bracts 25–30, eximbricate, in 2 series, mostly 3–4 mm long, oblong-lanceolate, prominently bicostate, with prominent antrorsely angular or lacerate scarious margins, the apex shortly to very sharply acute, usually not scarious near tip, the outer surface with usually few long hairs; receptacle naked; corolla white or blue, ca. 1.7 mm long, narrowly funnelform, with few hairs on the outer surface, the tube narrow, ca. 1 mm long, with scattered small short-stalked glands, the lobes 0.2–0.3 mm long, with papillae moderately developed inside, at tip and on margins, 1–2 hairs on outer surface; style branches extremely slender, sometimes short, with crowded blunt papillae

forming nearly ½ the width. *Achenes* ca. 1.2 mm long, with sparse short bristles usually restricted to the ribs; carpopodium asymmetrical; pappus of 5 large free scales, the scales usually lanceolate with long slender awns, to 2 mm long with awns.

Ageratum conyzoides is native in Central and South America and has become widely adventive in most tropical and many subtropical parts of the world. The species has been confused with *A. houstonianum* and differences are discussed under that species. The recent monograph by Johnson (1971) noted the unreliability of the pappus structure in this species and reduced to synonymy the species *A. latifolium* Cav., having awnless pappus scales. This latter species has been omitted from the present synonymy as further studies are required. Use of other characters such as corolla size and style branch structure show that some of the awnless material probably is *A. conyzoides* and some is *A. houstonianum* and still other material does not seem to be obviously either of these.

BOCAS DEL TORO: Changuinola, *Lazor et al. 2380* (FSU). Bocas del Toro, *Lazor et al. 2413* (FSU). SW of Bocas del Toro at Maccaw Hills, Isla Colón, 0–120 m, *von Wedel 427* (MO). Isla Colón, *von Wedel 2931* (MO, US). CANAL ZONE: Balboa, *Macbride & Featherstone 31* (F, US). Near Gatún, *Standley 27309* (US). Vic. of Summit, *Standley 30089* (US). CHIRIQUÍ: Boquete Lookout, 4000 ft, *D'Arcy & D'Arcy 6324* (MO). Boquete, *D'Arcy & D'Arcy 6349* (MO). Concepción, *King 5286* (US). Alto Boquete, 1125 m, *Partch 69–90* (MO). Vic. of San Félix, 0–120 m, *Pittier 5432* (US). COCLÉ: El Valle, *Dwyer 1839* (FSU, MO, US); *King 5327* (US). El Valle de Antón and vic., 500–700 m, *Seibert 473* (MO). DARIÉN: Puerto St. Dorotea, *Dwyer 2227* (MO). PANAMÁ: Isla Taboga, 0–350 m, *Allen 1277* (F, MO). 7 mi N of Cerro Azul on road to Cerro Jefe, 2600 ft, *Blum et al. 1757* (FSU). Cerro Campana, *Croat 12097* (MO). Cerro Azul, 2000 ft, *D'Arcy & D'Arcy 6217* (MO). Goofy Lake to ca. 8 mi S of Goofy Lake toward Cerro Jefe, *Dwyer 7055* (MO). SW facing slopes of Cerro Azul, *King 5248* (US). Cerro Campana, *Lazor 3324* (FSU). Altos del Río Pacora, 2500 ft, *Lewis et al. 2283* (MO). Chimán, *Lewis et al. 3366* (MO, UC). Taboga Island, *Longfield 488* (US); *Standley 27975* (US). Cerro Azul, 2000 ft, *Tyson 2057* (FSU), *2059A* (MO); ca. 2200 ft, *Tyson 6285* (FSU, MO, US); 2100 ft, *Tyson 6320* (FSU, MO). Cerro Jefe, *Tyson et al. 4298* (FSU, MO).

3. **Ageratum houstonianum** Miller, Gard. Dict., ed. 8. 1768. TYPE: Mexico, Veracruz, *Houston* (BM, not seen).—FIG. 13.

A. mexicanum Sims, Bot. Mag. 52: 2525. 1825. TYPE: Seed from Mexico, *Bullock* (K?, not seen).

Carelia houstoniana (Miller) Kuntze, Rev. Gen. Pl. 1: 325. 1891.

Ageratum wendlandii Vilm., Fl. Pl. Terre., ed. 4, suppl. 2. 1894. TYPE: Unnumbered figure, Fl. Pl. Terre., ed. 4, suppl. 2. 2. 1894 (Johnson, 1971).

Annual or short-lived perennial erect *herbs* or *subshrubs* to 0.9 m tall, sparingly branched; stems greenish to slightly reddish, terete, slightly striate, usually broadly fistulose, long-pilose and minutely puberulous. *Leaves* mostly opposite; blades broadly ovate to deltoid, to 10 cm long and 8 cm wide, the base usually truncate or slightly cordate, strongly trinervate, the margins crenate to serrate-crenate, the apex short-acute to narrowly rounded or obtuse, the upper surface dull green, sparsely long-pilose, the lower surface scarcely paler, sparsely long-pilose on the veins and veinlets, glandular punctations often lacking; petioles to 4 cm long. *Inflorescence* cymose to subcorymbose with densely corymbose to subumbellate branches, the branches densely puberulous with few to many longer hairs, the ultimate branches 1–8 mm long, not or scarcely enlarged distally. *Heads* 4.5–6.5 mm high with 50–75 florets; involucral bracts 20–30, eximbricate, in 2 series,

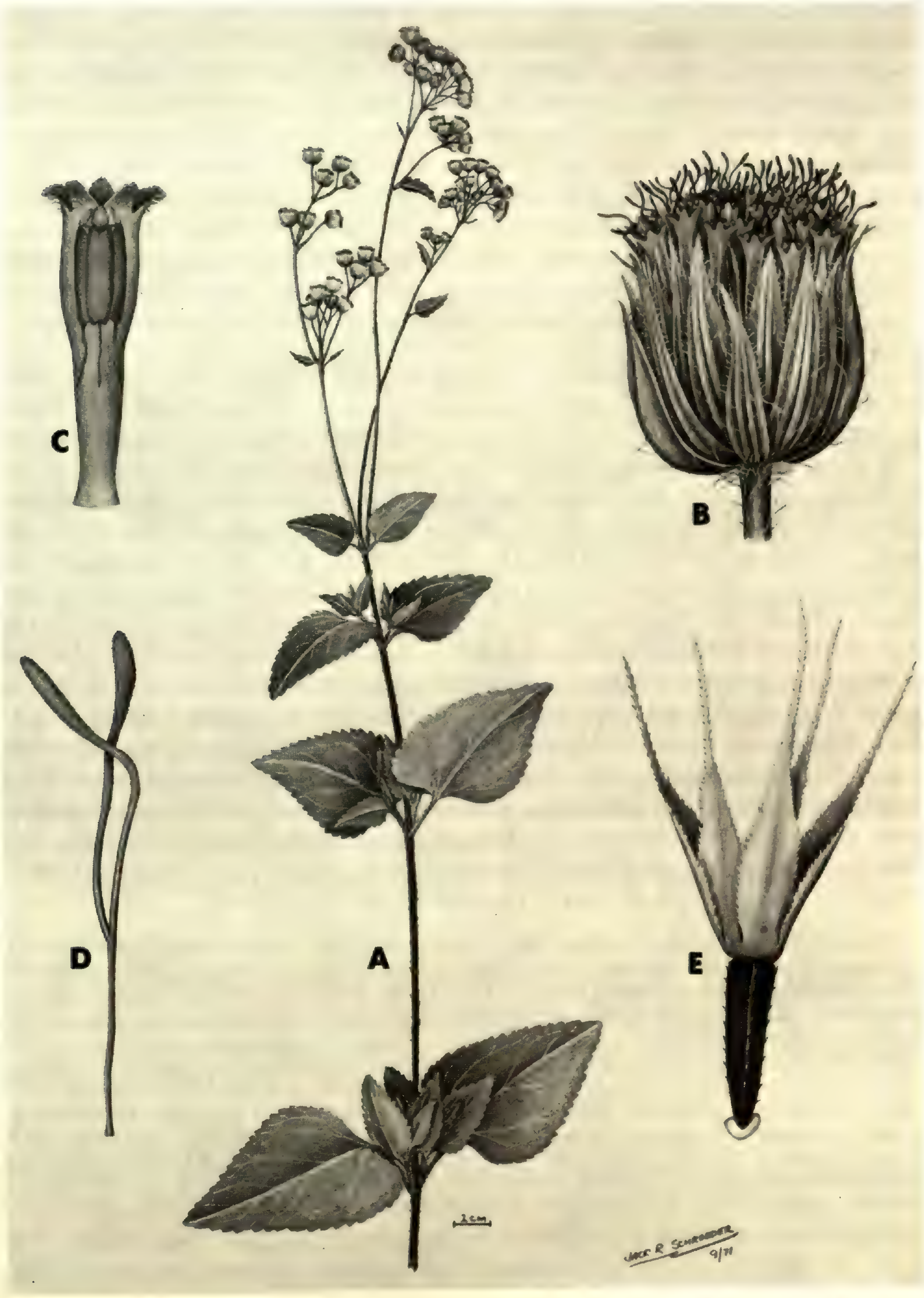

FIGURE 13. *Ageratum houstonianum* Miller.—A. Habit (× ½).—B. Head (× 47/10).—C. Corolla (× 14).—D. Style (× 14).—E. Achene (× 11⅘).

mostly 3.5–5.0 mm long, oblong-lanceolate to lanceolate, prominently bicostate, with scarious margins which are sometimes irregular above, the apex usually very sharply acute, rarely scarious near tip, the outer surface sparsely to densely pilose; receptacle naked; corolla and style branches usually bluish; corolla 2.3–3.0 mm long, narrowly funnelform, the somewhat tubular base ca. 1 mm long with a few minute glands, the limb usually glabrous, the lobes 0.3–0.4 mm long, papillae within, at the tip and on margins, many short hairs on outer surface; style branches slightly enlarged distally and usually very prominent, papillae small and somewhat pointed. *Achenes* ca. 1.2 mm long, with sparse short bristles usually restricted to the ribs; carpopodium asymmetrical; pappus of 5 large free scales, the scales usually lanceolate with a long slender apical awn, 2.0–2.5 mm long with awns.

Ageratum houstonianum is native in central and southern Mexico and southward into northern Central America. The species has become widely distributed in tropical and subtropical parts of the world, mostly escaping from cultivation. The species has been distinguished from *A. conyzoides* in previous treatments by the more pilose and more entire involucral bracts (Robinson, 1913; Grierson, 1972) and by the more truncate or cordate leaves (Johnson, 1971). However, these characters represent only weak trends. Material of *A. houstonianum* also tends to have a denser, less cymose inflorescence and less glandular-punctate leaf undersurfaces. Still, the most reliable differences are in the structure of the florets. The corollas of *A. houstonianum* are larger with more hairs on the lobes. Also, the corollas of *A. houstonianum* are as long as or longer than the awned pappus scales, while those of *A. conyzoides* are distinctly shorter. The style branches of *A. houstonianum* are thicker with smaller, more pointed papillae, and are usually very long exserted and bluish. The style branches of *A. conyzoides* are much more slender with nearly half the thickness being papillae, and the branches are often very short. The most obvious result of the basic differences of the species is that heads of *A. houstonianum* show mostly long, colored style branches while those of *A. conyzoides* show mostly exposed tips of pappus awns.

BOCAS DEL TORO: Along railroad near station at Milla 10, *Croat & Porter 16329* (MO). Almirante, *Gentry 2697* (MO). Bank of Río Changinola and Río Tararia, ca. 1 mi N of Changinola Banana Farm, *Lazor et al. 2432* (FSU, MO). 1.5 mi SE of Banana Plantation on Río Changinola, *Lazor et al. 2454* (FSU, MO). Abandoned field in Changuinola, *Lazor et al. 2596* (FSU). Farm 8 of Changinola Banana Plantation, United Fruit Company, *Lazor et al. 2587* (FSU, MO). Changuinola to 5 mi S at junction Ríos Changuinola & Terebé, 100–200 ft, *Lewis et al. 944* (MO, US). CANAL ZONE: Near Miraflores, *Greenman & Greenman 5200* (MO). Balboa, *Macbride & Featherstone 41* (F); *Standley 25665* (F, US), *30832* (US). CHIRIQUÍ: Boquete, *D'Arcy & D'Arcy 6346* (MO). 1 mi S of Volcán on the Cerro Punta Trail, *Lazor & Correa 2760* (FSU, MO). PANAMÁ: Sabanas N of Panama City, *Paul 589* (US). Juan Díaz, *Standley 30530* (US). Chepo, *Tyson 6769* (MO).

4. **Ageratum microcarpum** (Benth. in Örsted) Hemsl., Biol. Cent. Amer., Bot. 2: 82. 1881.

Coelestina microcarpa Benth. in Örsted, Vidensk. Meddel. Dansk Naturhist. Foren. Kjøbenhavn 1852: 72. 1852. SYNTYPES: Costa Rica, *Örsted* (C, not seen, US, photo).
Alomia microcarpa (Benth. in Örsted) B. L. Robinson, Proc. Amer. Acad. Arts 49: 452. 1913.

Annual or short-lived perennial erect *herbs* or *subshrubs* to 1.2 m tall, with few to many branches; stems becoming brownish to slightly reddish, terete,

slightly striate, sometimes broadly fistulose, sparsely to densely long-pilose, sometimes also slightly puberulous. *Leaves* mostly opposite; blades ovate, to 7 cm long and 4.5 cm wide, the base usually truncate to slightly cordate, strongly trinervate from the base, the margins closely serrate to serrate-crenate, the apex short-acute to slightly acuminate, the upper surface dull green, pilose with numerous long hairs, sometimes also sparsely puberulous, the lower surface slightly paler with glandular punctations and numerous long slender hairs; petioles to 3.5 cm long. *Inflorescence* corymbose to slightly cymose with compact corymbose branches, the branches densely whitish-puberulous to hirtellous, the ultimate branches 3–8 mm and rarely to 17 mm long. *Heads* 4–5 mm high with ca. 60–75 florets; involucral bracts ca. 25, eximbricate, in 2 series, ca. 4 mm long, oblong-lanceolate, prominently bicostate, with prominent often antrorsely lacerate scarious margins, the apex sharply acute, not scarious near tip, the outer surface pilose to hirtellous with numerous slender hairs; receptacle naked; corolla and style branches usually bluish; corolla ca. 2.3 mm long, the tube slender, ca. 1 mm long with numerous small but distinct stipitate glands, the limb and the upper tube usually with a few short hairs, the lobes ca. 0.3 mm long with many papillae inside and near the tip outside, a few short hairs on outer surface; style branches slightly enlarged distally and usually very prominent, papillae small and somewhat pointed. *Achenes* ca. 1.2 mm long, sparsely scabrid to essentially glabrous; carpopodium somewhat asymmetrical; pappus totally lacking.

Ageratum microcarpum is native in Central America from Honduras southward and in parts of northern South America. Though separated generically as *Alomia* in most treatments, the species is actually closely related to *A. conyzoides* and *A. houstonianum*. The species differs from its relatives by the complete lack of pappus, by the weakly scabrous or glabrous achenes and by the more numerous, more prominent glands on the corolla tube.

CHIRIQUÍ: Pasture above Boquete, 5200 ft, *D'Arcy & D'Arcy 6412* (MO).

5. **Ageratum oliveri** R. M. King & H. Robinson, Phytologia 28: 491. 1974. TYPE: Panama, Cerro Jefe, *Croat 13062* (MO, holotype; US, isotype).

Annual or short-lived perennial erect *herbs* or *subshrubs* to 1 m tall, with few branches; stems becoming brownish to slightly reddish, terete, slightly striate, usually broadly fistulose, sparsely to densely long-pilose, usually also slightly puberulous. *Leaves* mostly opposite; blades broadly ovate, to 9 cm long and 8 cm wide, the base of lower leaves usually slightly cordate, strongly trinervate from just above the base, the margins crenate to serrate-crenate, the apex shortly but distinctly acuminate, the upper surface yellowish- to dark green, smooth, pilose with numerous long hairs, the lower surface distinctly paler and fleshy with immersed glandular punctations, coarsely pilose only on veins and major veinlets; petioles to 4 cm long. *Inflorescence* cymose to subcymose with compact, corymbose to subumbellate branches, the branches densely short-puberulous, the ultimate branches 1–9 mm long, not noticeably enlarged distally. *Heads* ca. 5 mm high with ca. 60–75 florets; involucral bracts 20–25, eximbricate, in 2 series, mostly 3–4 mm long, lanceolate, bicostate, without evident scarious margins, the apex

sharply acute, the outer surface glabrous; receptacle naked; corolla and style branches blue; corolla 2.3–2.7 mm long, narrowly funnelform, the somewhat broad tube ca. 1 mm long with a very few minute glands on the outer surface, the limb glabrous, the lobes ca. 0.5 mm long with papillae inside and at the tip outside, a few short hairs on the outer surface; style branches not or only slightly broadened distally, long-exserted, with minute somewhat pointed papillae. *Achenes* ca. 1.5 mm long, glabrous; carpopodium asymmetrical; pappus completely lacking or forming a lobed serrulated coroniform rim to 0.3 mm high.

Ageratum oliveri seems endemic to the Cerro Azul–Cerro Jefe area of central Panama. The species has the habit and pilose stems of *A. houstonianum* but the upper and lower leaf surfaces, the lack of scarious margins on the involucral bracts, and the glabrous achenes with coroniform pappus all place the species in the section *Coelestina*. Notable species characters are the shortly acuminate, usually slightly cordate leaves and the glabrous involucre.

PANAMÁ: 7 mi N of Cerro Azul on road to Cerro Jefe, 2600 ft, *Blum et al. 1771* (FSU). Cerro Jefe along main road before turnoff to summit, *Croat 13062* (MO, US). Goofy Lake to ca. 8 mi S of Goofy Lake toward Cerro Jefe, *Dwyer 7055* (MO). Cerro Jefe, *Gentry 2867* (MO). Along road to Cerro Azul, 1600 ft, *Tyson 6328* (FSU, MO).

6. **Ageratum panamense** B. L. Robinson, Contr. Gray Herb. 104: 4. 1934, new name for *A. rivale* B. L. Robinson.

A. rivale B. L. Robinson, Contr. Gray Herb. 61: 3. 1920, not *A. rivale* Ses. & Moc., 1889. TYPE: Panama, vic. of El Boquete, Chiriquí, *Maxon 5240* (US, holotype; GH, isotype).

Erect to decumbent perennial *herb* or *subshrub* to 1.3 m tall, with few to many branches; stems becoming brownish to reddish, terete, slightly striate, solid to slightly fistulose, sparsely to somewhat densely puberulous or hirtellous. *Leaves* mostly opposite; blades ovate to ovate-lanceolate, to 7 cm long and 3 cm wide, the base rounded to short-cuneate, trinervate from just above the base, the margins somewhat closely serrate-crenate to serrulate, the apex acute or obtuse to narrowly rounded, not acuminate, the upper surface usually dark green, scarcely bullate, rather shiny, pilose with numerous long hairs, the lower surface pale to reddish, fleshy with immersed glandular punctations, coarsely pilose mostly on veins and veinlets; petioles mostly 2–5 mm long, rarely to 1 cm long in lower leaves. *Inflorescence* with few or no long branches, ending in compact corymbose to subumbellate clusters, the branches densely whitish puberulous, the ultimate branches 3–30 mm long, not noticeably enlarged distally. *Heads* 5–7 mm high with ca. 50–100 florets; involucral bracts 20–30, eximbricate, in 2 series, mostly 4–6 mm long, broadly to narrowly lanceolate, bicostate, without distinct scarious margins, with short marginal hairs more numerous near tip, the apex sharply acute, the outer surface nearly glabrous or with a few short hairs; receptacle naked; corolla and style branches usually bluish; corolla 2.5–3.5 mm long, narrowly funnelform, the tube rather broad and indistinct, glabrous or with a few minute glands, the limb glabrous, the lobes ca. 0.5 mm long with papillae on inner surface and on the slight outer tip, 1–2 short hairs on outer surface; style branches very slender, not or only slightly enlarged distally, prominent, with minute pointed

papillae. *Achenes* 1.5–2.5 mm long, glabrous; carpopodium slightly asymmetrical; pappus coroniform or of irregular broad scales to 0.4 mm long, sometimes with a single awn to 2.5 mm long.

As delimited here the species is apparently endemic to western and central Panama. *Ageratum panamense* is notable for the nonpilose stems and the short petioles. The recent monograph by Johnson (1971) placed the species in the synonymy of the obscure *A. riparium* B. L. Robinson of Costa Rica. The original description and key characters of the latter, however, indicate a plant with significant differences: acuminate leaves, petioles 1 cm long, lower leaf surface not much paler, corolla tubes slender, and achenes sometimes hispid on the basal angles. A more closely related species, *A. petiolatum* (Hook. & Arn.) Hemsl., (including *A. reedii* R. M. King & H. Robinson) of Nicaragua and Costa Rica differs by the longer leaf petioles and by the narrower, more pilose involucral bracts.

CHIRIQUÍ: Boquete region Alto Lino, 4200 ft, *Maurice 874* (US). Alto Boquete, *Correa 427* (MO). Cerro Pando, ca. 6000 ft, *D'Arcy & D'Arcy 6502* (MO). Boquete, *Davidson 590* (F, MO, US). Boquete, roadway at Hotel Dos Ríos, ca. 4000 ft, *Dwyer & Hayden 7568* (MO). Río Caldera S of El Boquete, 1250 m, *Killip 3612* (US). Road to Cerro Punta, ca. 25 mi N of Concepción, *King 5289* (US), 4.3 km S of Volcán along drainage to Las Lagunas, *Lazor & Correa 2829* (FSU, MO). Vic. of Boquete, from Boquete to 3 mi N, 3300–4200 ft, *Lewis et al. 313* (MO, US). Vic. of El Boquete, 1000–1300 m, *Maxon 5240* (US). Pastures around El Boquete, 1000–1300 m, *Pittier 2905* (US). Llanos del Volcán, 1120–1200 m, *Seibert 342* (MO, US). Nueva California, 4000 ft, *Tyson 5717* (FSU, MO). Río Chiriquí Viejo valley, near El Volcán, *White 222* (MO, US). Vic. of Boquete, 1200–1500 m, *Woodson & Schery 734* (MO). Finca Lerida to Boquete, ca. 1300–1700 m, *Woodson et al 1102* (MO), *1147* (MO, US). COCLÉ: El Valle de Antón, *Maurice 777* (US). El Valle, *Dwyer 1826* (MO). El Valle de Antón, *Hunter & Allen 377* (MO). El Valle de Antón and vic., 500–700 m, *Seibert 472* (MO, US). Between Las Margaritas and El Valle, *Woodson et al. 1767* (MO, US). PANAMÁ: Finca Indio, Cerro Azul region, *D'Arcy & D'Arcy 6245* (MO).

13. AUSTROEUPATORIUM

Austroeupatorium R. M. King & H. Robinson, Phytologia 19: 433. 1970. TYPE: *Eupatorium inulaefolium* H.B.K.

Erect perennial *herbs* or *subshrubs*, with few branches. Lower *leaves* opposite, upper leaves often subopposite or alternate, with short petioles; blades ovate to narrowly oblong, the margins usually crenulate to serrulate. *Inflorescence* a flattened corymbose panicle. *Heads* discoid with 9–23 florets; involucral bracts 12–18, mostly unequal, subimbricate, in 2–3 series, spreading at maturity; receptacle glabrous, plane or slightly convex; corolla narrowly funnelform with somewhat narrow tube, glands on outer surface, the cells of the corolla narrow with sinuous walls, the lobes without papillae or stomata; anther collars narrow with mostly quadrate or short-oblong cells, the walls with prominent annular thickenings, the exothecial cells quadrate, the anther appendage longer than wide; style base densely hirsute, not inflated, the style appendages linear, covered with short papillae. *Achenes* prismatic with 5 ribs, usually with glands, without bristles; carpopodium distinctly enlarged, sometimes elongate, the cells enlarged with thin walls; pappus of 30–40 slender scabrous bristles in one series, persistent, the apical cells often enlarged and blunt. *Pollen* with short spines.

The genus contains about 11 species found mainly in South America. One species has been collected in Panama and is also adventive in some parts of the Old World.

Literature:

King, R. M. & H. Robinson. 1970. Studies in the Eupatorieae (Compositae). XXVI. A new genus *Austroeupatorium*. Phytologia 19: 433–435.

1. **Austroeupatorium inulaefolium** (H.B.K.) R. M. King & H. Robinson, Phytologia 19: 434. 1970.—FIG. 14.

Eupatorium inulaefolium H.B.K., Nov. Gen. Sp. Pl. 4: 85. ed. fol. 1818. TYPE: Colombia, near Mariquita, *Humboldt & Bonpland* (P, not seen, US, photo).
E. molle H.B.K., Nov. Gen. Sp. Pl. 4: 85. ed. fol. 1818. TYPE: Colombia, near Mariquita, *Humboldt & Bonpland* (P, not seen, US, microfiche).
E. suaveolens H.B.K., Nov. Gen. Sp. Pl. 4: 86. ed. fol. 1818. TYPE: Colombia, near Sant-Anna, Mariquita and Ibague, *Humboldt & Bonpland* (P, not seen, US, microfiche).
E. paranense Hook. & Arn., Companion Bot. Mag. 1: 241. 1836. SYNTYPES: Brasil, Paraná, *Tweedie*. Argentina, Buenos Aires, *Tweedie* (both K, not seen).
E. pallidum Hook. & Arn., Companion Bot. Mag. 1: 241. 1836. SYNTYPES: Argentina, Buenos Aires, *Tweedie*. Argentina, San Isedro, *Tweedie* (both K, not seen).
E. pallescens DC., Prodr. 5: 154. 1836. TYPE: Brasil, Minas Geraes, *Vauthier 273* (G-DC, not seen, US, photo).
E. decemflorum DC., Prodr. 5: 154. 1836. TYPE: Peru, *Poeppig* (G-DC, not seen, US, microfiche).
E. silphiifolium Mart., Flora 20, Beibl. 2: 105. 1838. TYPE: Brasil, Rio de Janeiro, *Martius* herb. no. 140 (NY).
E. ramosissimum Gardn., London Jour. Bot. 6: 441. 1847. TYPE: Brasil, margins of woods near Villa de Arrayas, Goyaz, *Gardner 4206* (BM, not seen).
E. horsfieldii Mig., Fl. Bat. 2027. 1856. TYPE: Java, *Horsfield* (U, photo US).
E. cinereum Griseb., Fl. Brit. W. Ind. 359. 1861. TYPE: Trinidad, *Crueger* (GOET, not seen; K, not seen).

Erect perennial *herbs* or *subshrubs* to 3 m tall, with few branches; stems brownish, terete, slightly striate, densely puberulous to tomentulose. *Leaves* mostly opposite; blades narrowly ovate to lanceolate, to 15 cm long and 6 cm wide, the base rounded to cuneate and abruptly narrowed, the margins slightly serrulate to crenate-serrate, the apex narrowly acuminate, the upper surface smooth to slightly bullate, sparsely to densely puberulous, the lower surface densely puberulous to tomentellous with numerous glandular punctations, the venation prominently trinervate from near the base; petioles short, to 15 mm long, becoming winged distally. *Inflorescence* broadly and densely corymbose, the ultimate branches short and tomentellous, to 3 mm long. *Heads* 6–7 mm high with 8–15 florets; involucral bracts 12–15, subimbricate, in ca. 3 series, suborbicular to broadly oblong, 1.5–6.0 mm long, short-acute to rounded with scarious tips and margins, weakly 2–4 costate, the exposed outer surfaces puberulous; corolla white, 4.0–4.5 mm long, the slender tube ca. 1.5 mm long, some glands on tube and lobes, the lobes short, about as broad as long, sometimes with 1–2 small hairs. *Achenes* 1.8–2.0 mm long, glabrous or with a few glands; carpopodium short and broad, the cells large and thin-walled in ca. 7 rows; pappus of 30–40 slender bristles, 3.5–4.0 mm long, the apical cells blunt, not broadened. *Pollen* 18–20 μ in diameter.

FIGURE 14. *Austroeupatorium inulaefolium* (H.B.K.) R. M. King & H. Robinson.—A. Habit (× ½).—B. Head (× 4⅗).—C. Corolla (× 9⅕).—D. Achene (× 9⅕).—E. Style (× 9⅕).

Austroeupatorium inulaefolium has not been previously reported from Panama but it is widely distributed in South America and is adventive in the Eastern Hemisphere in Indonesia and Ceylon. One of the distinctive characters of the species is the very large, broad carpopodium with large, thin-walled cells. A few species of South America, *A. mapirense* (Hieron.) R. M. King & H. Robinson and *A. monardifolium* (Uslp.) R. M. King & H. Robinson, seem very close but

reportedly differ by the under surface of the leaves being very short-puberulous or nearly glabrous between the vein reticulations.

PANAMÁ: 1 mi W from Su-Lin Motel along dirt road to Cerro Campana, *Correa & Dressler 366* (MO). Roadside on way to Cerro Campana, *Croat 12021* (MO). SW facing slopes of mts. E of Chica, *King 5266* (US).

14. AYAPANA

Ayapana Spach, Hist. Veg. Phan. 10: 290. 1841. TYPE: *A. officinalis* Spach = *A. triplinervis* (Vahl) R. M. King & H. Robinson.

Lepidesmia Klatt, Bull. Herb. Boissier 4: 479. 1896. TYPE: *L. squarrosa* Klatt.
Tamayoa Badillo, Bol. Soc. Venez. Ci. Nat. 9: 139. 1944. TYPE: *T. paraguanensis* Badillo.

Erect perennial *herbs*, unbranched or basally branched. *Leaves* mostly opposite, sessile or winged to base; blades narrowly ovate to elliptical entire to serrulate, pinnately or trinervately veined. *Inflorescence* laxly paniculate with corymbose to subcymose branches. *Heads* discoid with 5–40 florets; involucre of 15–35 lanceolate subimbricate bracts, in 2–5 series, spreading when mature, the innermost bracts deciduous; receptacle convex, glabrous (paleaceous in one species); corolla narrowly funnelform or tubular, internally glabrous, with glands externally on the lobes, the cells of the corolla elongate with sinuous walls, the lobes short-triangular; anther collars slender, the cells mostly elongate with transverse annular thickenings in the walls, the exothecial cells subquadrate, the anther appendage triangular or oblong, longer than wide; style base with distinct enlarged node, the style branches without glands, the appendages tapering, often strongly curled, with prominently projecting papillae. *Achenes* prismatic, 5-ribbed, with few to many bristles mostly on the ribs; carpopodium enlarged and sharply delimited, the cells thick-walled, in many series, the basal series of cells greatly enlarged; pappus of ca. 18–30 slender scabrous sometimes fragile bristles (reduced to short bristles or scales in one species, *A. squarrosa*), the bristles not enlarged distally, the apical cells sharply pointed. *Pollen* with short sharp spines.

Ayapana contains 11 species ranging from Costa Rica into South America and the West Indies. The greatest concentration of species is in the Andean region. One species, *A. squarrosa* (Klatt) R. M. King & H. Robinson, has been incorrectly placed in a distinct genus (*Lespidesmia*) and even transferred to the tribe Heliantheae by previous writers because of the combination of reduced style appendages, paleaceous receptacle and reduced papus. Three species of *Ayapana* have been collected in Panama.

A related genus, *Polyanthina*, has been found in Costa Rica and Colombia and may be expected at higher elevations in western Panama. The single species, *P. nemorosa* (Klatt) R. M. King & H. Robinson, has the winged or sessile leaf bases and the distinctive carpopodium found in *Ayapana* but differs by the heads having 200–300 slender florets, the receptacle being pubescent and the style branches being linear and scarcely papillose.

Literature:

King, R. M. & H. Robinson. 1970. Studies in the Eupatorieae (Compositae). XXX. The genus, *Ayapana*. Phytologia 20: 210–212.

a. Leaves narrowly acuminate at tip; florets whitish; corolla with short broad lobes ..... 2. *A. elata*

aa. Leaves obtusely acute to rounded at tip; florets reddish or purplish; corolla with lobes distinctly longer than wide.

b. Leaves sessile or very shortly petiolate; heads with ca. 25 florets ..... 3. *A. stenolepis*

bb. Leaves usually with narrow petioliform bases; heads with 30–40 florets ..... 1. *A. amygdalina*

1. **Ayapana amygdalina** (Lam.) R. M. King & H. Robinson, Phytologia 20: 211. 1970.—Fig. 15.

Eupatorium amygdalinum Lam., Encycl. Méth. 2: 408. 1788. TYPE: Peru, *J. Jussieu*, Herb. Jussieu no. 8393 (P, not seen, US, microfiche).

E. loniceroides H.B.K., Nov. Gen. Sp. Pl. 4: 91. ed. fol. 1818. TYPE: Colombia, between Popayán and Pindamon, *Humboldt & Bonpland* (P, not seen, US, microfiche).

E. salzmannianum DC., Prodr. 5: 159. 1836. TYPE: Brasil, Bahia, *Salzmann* (G-DC, not seen, US, photo).

E. dodonaeaefolium DC., Prodr. 5: 161. 1836, not *E. dodoneaefolium* Hook. & Arn. TYPE: Peru, *Poeppig 1832* (G-DC, not seen, US, microfiche).

E. subobtusum DC., Prodr. 5: 161. 1836. TYPE: Brasil, Bahia, *Blanchet 1409* (G-DC, not seen, US, photo).

E. oxychlaenum DC., Prodr. 5: 162. 1836. TYPE: Brasil, Minas Geraes, *Vauthier 280* (G-DC, not seen, US, microfiche).

E. ixodes Benth., Jour. Bot. (Hooker) 2: 41. 1840. TYPE: British Guiana, savannahs of the Rupunoony, *Schomburgk 79* (NY).

E. barclayanum Benth., Bot. Voy. Sulphur 112. 1845. TYPE: Panama, Isle of Taboga, Bay of Panama, *Belcher et al.* (BM, not seen).

Bulbostylis elegans Gardn., London Jour. Bot. 5: 467. 1846. SYNTYPES: Brasil, Serra da Batalha, Pernambuco, *Gardner 2899*. Brasil, Rio Clara, Minas Geraes, *Gardner 4843* (both BM, not seen).

B. tomentosa Gardn., London Jour. Bot. 5: 468. 1846. TYPE: Brasil, Diamond District, Minas Geraes, *Gardner 4844* (BM, not seen).

B. microcephala Gardn., London Jour. Bot. 5: 468. 1846. TYPE: Brasil, Serra de Araripé, Ceará, *Gardner 1734* (BM, holotype, not seen; US, isotype).

B. glandulosa Gardn., London Jour. Bot. 5: 469. 1846. TYPE: Brasil, Minas Geraes, *Gardner s.n.* (BM, not seen).

B. micrantha Gardn., London Jour. Bot. 6: 449. 1847, nom. nud. TYPE: Brasil, Goyaz, *Gardner 3269* (BM, not seen).

Eupatorium glandulosissimum Malme, Kongl. Svenska Vetenskapsakad. Handl. 32 (5): 40. 1899. TYPE: Brasil, Buriti, Serra da Chapada, Matto Grosso, *Malme 1744* (S).

Coarse perennial *herbs* or *subshrubs* mostly 1.5–2.0 m high, unbranched or mostly branched at base; stems becoming brownish to reddish, terete or somewhat hexagonal, glabrate to densely puberulous or stipitate glandular. *Leaves* slightly to distinctly imbricated, sessile or very short-petiolate, oblong to obovate, mostly 5–10 cm long and 2–3 cm wide, the lower leaves to 16 cm long and 5.5 cm wide, the base cuneate, sometimes with slight auricles, the margins entire to crenate-serrate, the apex rounded to short-acute, the upper surface obscurely and the lower surface more prominently glandular punctate, the surfaces glabrate to densely hirsute or stipitate glandular, the venation pinnate with ascending secondary veins. *Inflorescence* openly corymbose-paniculate with corymbose to subcymose branches, the branches glabrate to densely stipitate glandular, the ultimate branches 1–20 mm long. *Heads* 7–10 mm high with 30–40 florets; involucral bracts usually partly reddish, ca. 30–40, subimbricate, in 4–5 series, 1–9 mm long, mostly narrowly oblong to linear with little or no scarious margin, the apex short-acute or apiculate to long-attenuate, the outer surface puberulous to densely stipitate

FIGURE 15. *Ayapana amygdalina* (Lam.) R. M. King & H. Robinson.—A. Habit (× 2/5).—B. Base of plant (× 2/5).—C. Head (× 4 2/5).—D. Achene (× 12 3/10).—E. Corolla (× 12 3/10).—F. Style (× 12 3/10).

glandular; corolla reddish, 6–8 mm long, narrowly funnelform, glabrate below, the lobes 0.5–1.0 mm long, longer than wide, with glands and sometimes a few hairs on outer surface. *Achenes* 1.5–2.3 mm long, with numerous bristles mostly on the ribs; pappus of 20–25 slender bristles.

Ayapana amygdalina is distributed from Nicaragua south to Bolivia and Brazil. The species is rather uniform through much of the range, with glabrate stems, leaves, and inflorescence and with short-acute or apiculate involucral bracts. Much of the variation occurs in Brasil where some plants are densely stipitate glandular and many have long-attenuate involucral bracts.

On Taboga Island this species has the common name of "Colindre", *Standley 28011* (US).

CANAL ZONE: Sabanas along Río Azote Caballo, 66–70 m, *Dodge et al. 16841* (F, MO). Road to Corozal, *Gervais 147* (US). Ancón hill, *Greenman & Greenman 5097* (MO); *Piper 5571, 5582* (both US). Sabana de Marcelito, near El Vigia, *Pittier 2383* (US). Ancón hill, *Standley 26343* (US). CHIRIQUÍ: 12 mi N of Puerto Armeulles, ca. 100 m, *Croat 21877* (MO). COCLÉ: Picacho de Ola, 350–600 m, *Pittier 5059* (US). PANAMÁ: Isla Taboga, 0–350 m, *Allen 1278* (F, MO). Hills above Campana, 600–800 m, *Allen 1313* (MO). Road to Cerro Campana, *Correa & Dressler 835* (MO). Cerro Jefe, 2900 ft, *Dwyer et al. 7291* (MO). Cerro Campana, *Dwyer et al. 4706* (MO). Sabanas near Chepo, 30 m, *Hunter & Allen 74* (MO). SW slopes of mts. just E of Chica, *King 5267* (US). SE slope of Cerro Campana, *Lewis et al. 3136* (MO). 7 mi S of Campana, 3–30 m, *McDaniel 8312* (FSU, US). Taboga Island, *Miller 2029* (US). Sabanas, N of Panama City, *Paul 626* (US). Taboga Island, *Pittier 3589* (US). Cerro Campana, *Porter et al. 4324* (MO). Near the big swamp E of the Río Tocumen, *Standley 26644* (US). Taboga Island, *Standley 28011* (US). SE slope of Cerro Jefe, 2700 ft, *Tyson 3549* (MO). Cerro Campana, 1500 ft, *Wilbur & Weaver 11311* (F, MO, US).

2. **Ayapana elata** (Steetz) R. M. King & H. Robinson, Phytologia 27: 235. 1973.

Eupatorium elatum Steetz in Seem., Bot. Voy. Herald 148. 1854. TYPE: Panama, *Seemann 448* (BM, not seen, US, photo).

E. sprucei B. L. Robinson, Proc. Amer. Acad. Arts 55: 33. 1919. TYPE: Peru, River Huallaga, *Spruce 4167* (GH, holotype; B, isotype, destroyed, US, photo).

Coarse perennial *herbs* to 3 m tall, unbranched or branching from base; stems greenish or pale brownish, mostly hexagonal, slightly striate, rather densely minutely puberulous. *Leaves* usually laxly imbricate, opposite, narrowly elliptical to lanceolate, to 25 cm long and 7 cm wide, the base petioliform with narrow wing, auriculate at base, becoming wider and indistinct above, the margins entire to serrulate, sometimes somewhat crenate-serrate below the middle, the apex narrowly and sharply acuminate, the upper surface glabrate with sparse small hairs, the lower surface glandular-punctate and puberulous with short hairs, the venation pinnate with secondary veins ascending. *Inflorescence* paniculate with laxly subcymose branches, the ultimate branches mostly 3–7 mm long, densely puberulous. *Heads* ca. 5 mm high with 20–25 florets; involucral bracts ca. 25, subimbricate, in ca. 3 series, 1.0–4.5 mm long, ovate to oblong with broadly scarious margins, the apex rounded to obtusely acute, the outer surface with few glandular punctations, puberulous on exposed parts; corolla white to greenish, ca. 3 mm long, narrowly funnelform, glabrate, the lobes ca. 0.2 mm long and wide, densely glanduliferous on outer surface. *Achenes* ca. 1.5 mm long, with numerous bristles mostly on the ribs; pappus of ca. 35 slender bristles.

Ayapana elata is known primarily from Costa Rica, Panama, and Peru. The species may occur in Colombia but is obviously not common there. The species is not as remarkably disjunct as the related *A. stenolepis*.

BOCAS DEL TORO: Changuinola Valley, *Dunlap 455A* (F, US). CANAL ZONE: Barro Colorado Island, *Croat 8378* (MO). Chagres, *Fendler 157* (MO, US). Militar Reserva Fuerta

Sherman and adjacent Canal Zone S-1 between Gatún and Piña, 0–170 m, *Liesner 1349* (MO). Barro Colorado Island, *Shattuck* (F); *Woodworth & Vestal 600* (F). CHIRIQUÍ: 10–11 mi W of Puerto Armuelles in vic. of San Bartolo Limite, 300–500 m, *Croat 22015* (MO). COCLÉ: El Valle, *Croat 14265* (MO). La Mesa above El Valle, 900 m, *Croat 22975* (MO). 2 mi N of Cerro Pilón, 900 m, *Liesner 713A* (MO). PANAMÁ: Road to Cerro Campana, *Correa & Dressler 843* (MO). Cerro Campana, *Croat 14214* (MO); *Dwyer et al. 4839* (MO). 2 mi up Cerro Campana, *Lazor 2228* (FSU, MO).

3. **Ayapana stenolepis** (Steetz) R. M. King & H. Robinson, Phytologia 32: 284. 1975.

Eupatorium stenolepis Steetz in Seemann, Bot. Voy. Herald 148. 1853. TYPE: Panama, Veraguas, *Seemann 1135* (BM).
E. pyramidale Klatt, Abh. Naturf. Ges. Halle 15: 324. 1882. TYPE: Bolivia, Prov. Chiquitos, Santa Cruz, *d'Orbigny 680* (GH; G, not seen, US, photo).
Ayapana pyramidalis (Klatt) R. M. King & H. Robinson, Phytologia 20: 212. 1970.

Coarse perennial *herbs* or *subshrubs* to 1 m tall, branching mostly from the base; stems becoming pale brown, terete, striate, densely hirtellous with minutely gland-tipped hairs. *Leaves* usually crowded and much imbricated, opposite, oblong-elliptical to oblanceolate, 4–12 cm long and 0.7–2.0 cm wide, the base sessile, usually narrowly cuneate and somewhat petioliform, the margins entire or subentire, the apex obtuse with a mucro, the upper and lower surfaces obscurely glandular-punctate and densely hirtellous with minutely gland-tipped hairs, the venation pinnate with ascending secondary veins. *Inflorescence* paniculate with somewhat densely corymbose branches, the branches densely hirtellous with minutely gland-tipped hairs, the ultimate branches 1–8 mm long. *Heads* 7–8 mm high with 21–25 florets; involucral bracts ca. 25, subimbricate, in 2–3 series, 2–6 mm long, linear with little or no scarious margin, the apex attenuate with many nonglandular hairs, the outer surface covered with stipitate glands; corolla reddish to lavender, ca. 5 mm long, narrowly funnelform, glabrate, the lobes 0.5–0.7 mm long, longer than wide, sparsely glanduliferous on outer surface. *Achenes* 1.2–1.5 mm long, with numerous bristles mostly on the ribs; pappus of ca. 25 slender bristles.

The Bolivian material closely matches that from Panama and there are no known collections of the species from areas between. Material of *Eupatorium amygdalinum* var. *revolutum* Baker of Brazil may be the same species.

HERRERA: Vic. of Las Minas, La Peña, *Stern et al. 1781* (MO, US). VERAGUAS: Santiago, *Seemann 1135* (BM).

15. BARTLETTINA

Bartlettina R. M. King & H. Robinson, Phytologia 22: 160. 1971, new name for *Neobartlettia* R. M. King & H. Robinson.

Neobartlettia R. M. King & H. Robinson, Phytologia 21: 294. 1971, not *Neobartlettia* Schlechter (Orchidaceae). TYPE: *Eupatorium tuerckheimii* Klatt.

Shrubs or small *trees*, laxly branching. *Leaves* opposite with long slender petioles; blades ovate to lanceolate, the base cuneate to truncate, never cordate, the surface often with glandular punctations. *Inflorescence* mostly laxly corymbose-paniculate. *Heads* discoid with 20–150 florets; involucral bracts 20–50,

subimbricate to imbricate, unequal, in 3–5 series, spreading at maturity, the innermost bracts deciduous; receptacle convex, glabrous or with short hairs, corolla tubular, narrowly funnelform above, the inner and outer surfaces smooth, the cells of the corolla mostly narrow with sinuous walls, the lobes short-triangular with hairs or glands on outer surface; anther collars very elongate with numerous quadrate or short-rectangular cells below, the cell walls inornate, the exothecial cells quadrate or wider than long, the anther appendage oblong-ovate to long-triangular; style without basal enlargement, glabrous, the style appendages slender or very narrowly clavate at tip, nearly smooth or short-papillose. *Achenes* prismatic with 5 ribs, usually glabrous or with sparse bristles; carpopodium somewhat enlarged with smaller cells near the base, the larger upper cells continuous into enlarged bases of the ribs, the cell walls thin; pappus of 30–40 slender bristles in 1–2 series, scabrous, persistent, the apical cells acute.

Bartlettina is a genus of 20 species ranging from Mexico and Central America to northern South America and Brazil. The center of speciation is in Central America. Three species have been collected in Panama.

Literature:

King, R. M. & H. Robinson. 1971a. Studies in the Eupatorieae (Asteraceae). XXXVI. A new genus, *Neobartlettia*. Phytologia 21: 294–297.

——— & ———. 1971b. Studies in the Eupatorieae (Asteraceae). LXI. Additions to the *Hebeclinium* complex with *Bartlettina*, a new generic name. Phytologia 22: 160–162.

a. Leaf blades trinervate from the base; heads large and prominent with 40–50 involucral bracts and 60–75 florets; involucral bracts with 4–8 distinct costae; corollas with only glands on outer surface ——— 2. *B. platyphylla*

aa. Leaf blades somewhat trinervate from the basal fourth or fifth; heads smaller with 20–25 involucral bracts and 20–25 florets; involucral bracts with only a few indistinct costae; corollas with few to many hairs on outer surface.

b. Leaf blades broadly ovate with abruptly short-acuminate tips and truncate or short-cuneate bases; corollas 5–6 mm long with numerous hairs covering upper part; pappus bristles extremely slender in distal half; stems mostly fistulose ——— 1. *B. maxonii*

bb. Leaf blades ovate or narrowly ovate with narrowly acuminate tips and cuneate to narrowly cuneate bases; corollas 4–5 mm long with hairs mostly restricted to the outer surface of lobes; pappus bristles often as thick or thicker in distal half as near base; stems with pith mostly solid ——— 3. *B. prionophylla*

1. **Bartlettina maxonii** (B. L. Robinson) R. M. King & H. Robinson, Phytologia 22: 161. 1971.

Eupatorium maxonii B. L. Robinson, Proc. Amer. Acad. Arts 54: 251. 1918. TYPE: Panama, El Boquete, Chiriquí, *Maxon 4942* (US, holotype; GH, US, isotypes).
Neobartlettia maxonii (B. L. Robinson) R. M. King & H. Robinson, Phytologia 21: 296. 1971.

Shrub 3–4 m tall, freely and divaricately branched; stems grayish-brown, terete to subquadrangular, slightly striate, densely minutely puberulous, the stems mostly fistulose. *Leaves* opposite; blades broadly ovate, to 14 cm long and 11 cm wide, the base truncate or short-cuneate, the margins sharply serrate, sometimes with a dentation near basal third, the apex abruptly short-acuminate, the surface minutely and sparsely puberulous with scattered glandular punctations, the

venation somewhat trinervate from the basal third; petioles slender, to 8 cm long. *Inflorescence* corymbose-paniculate, the ultimate branches 2–7 mm long, minutely puberulous; receptacle glabrous. *Heads* ca. 10 mm high with 20–25 florets; the base of the involucre with 1–3 small linear-lanceolate bracts; involucral bracts ca. 23, subimbricate, in ca. 3 series, ovate to oblong with short-acute tips, the outer surface with 2–6 somewhat indistinct costae, minutely puberulous, often with glandular punctations; corolla lavender, 5–7 mm long, the upper corolla covered with many fine hairs, the lobes short, broader than long. *Achenes* ca. 1.5 mm long, glabrous; pappus of ca. 40 fine bristles.

Bartlettina maxonii is endemic to western Panama. The species seems closely related to *B. prionophylla* which grows in the same general area but at distinctly higher elevations.

CHIRIQUÍ: El Boquete, 1000–1300 m, *Maxon 4942* (US, GH).

2. **Bartlettina platyphylla** (B. L. Robinson) R. M. King & H. Robinson, Phytologia 22: 161. 1971.—FIG. 16.

Eupatorium platyphyllum B. L. Robinson, Proc. Amer. Acad. Arts 35: 339. 1900. TYPE: Mexico, near Chicharras, Chiapas, *Nelson 3765* (GH, not seen; US).
Neobartlettia platyphylla (B. L. Robinson) R. M. King & H. Robinson, Phytologia 21: 296. 1971.

Shrubs or small *trees* to 5 m tall, with few branches; stems brownish to reddish-brown, terete, scarcely striate, hirtellous in younger parts, the pith solid. *Leaves* opposite; blades broadly ovate, to 15 cm long and 12 cm wide, the base truncate or short-cuneate, the margins serrate to slightly doubly serrate, the apex narrowly short-acuminate, the surface glabrate, sparsely glandular-punctate, the venation trinervate from the base; petioles slender, to 9 cm long. *Inflorescence* pyramidally corymbose-paniculate with large heads usually contiguous when pressed, the ultimate branches 0.5–2.5 cm long, hirtellous; receptacle glabrous. *Heads* 15–20 mm high and ca. 10 mm wide with 60–75 florets; involucral bracts ca. 40–50, imbricate, in 4–5 series, broadly ovate to oblong with rounded sometimes erose or reflexed tips, the outer surface glabrous, with 4–8 distinct costae, a few linear deciduous inner bracts; corolla white, mostly 6–8 mm long, with only a few capitate glands on outer surface of lobes. *Achenes* ca. 2 mm long, usually completely glabrous; pappus of ca. 60 fine bristles in 2 series.

The species ranges from central Mexico south to Panama. It has often been confused with the superficially similar looking genus *Schistocarpha* of the Heliantheae.

CHIRIQUÍ: Trail from Paso Ancho to Monte Lirio, upper valley of Río Chiriquí Viejo, 1500–2000 m, *Allen 1583* (F, MO, US). Palo Santo, 3 mi N of Volcán, *Croat 13584* (MO). 1 mi E of Cañas Gordas, near Costa Rican border on road to Volcán, 800–1200 m, *Liesner 277* (MO). Vic. of El Boquete, 1000–1300 m, *Maxon 5051* (US). El Boquete, 1000–1300 m, *Pittier 2941* (US). Las Lagunas, 2 mi SW of El Volcán, 4200 ft, *Tyson 863* (FSU).

3. **Bartlettina prionophylla** (B. L. Robinson) R. M. King & H. Robinson, Phytologia 22: 161. 1971.

Eupatorium prionophyllum B. L. Robinson, Proc. Amer. Acad. Arts 36: 484. 1901. TYPE: Costa Rica, banks of Río Toros, *Pittier 1705* (GH, not seen).

FIGURE 16. *Bartlettina platyphylla* (B. L. Robinson) R. M. King & H. Robinson.—A. Habit (× 2/5).—B. Head (× 2 1/5).

Neobartlettia prionophylla (B. L. Robinson) R. M. King & H. Robinson, Phytologia 21: 296. 1971.

Shrub or small *tree* 2–3 m tall, laxly branched; stems brownish, mostly terete, slightly striate, densely minutely puberulous, the pith usually solid. *Leaves* opposite; blades ovate to narrowly ovate, to 11 cm long, usually to 6 cm wide,

rarely to 8 cm wide, the base short- to long-cuneate, the margins sharply and irregularly serrate, sometimes doubly serrate, the apex gradually sharply acuminate, the surface minutely and sparsely puberulous, with scattered glandular punctations, the veins sometimes rather trinervate with 1–2 pairs of ascending secondary veins in the basal fourth; petioles slender, to 5 cm long. *Inflorescence* corymbose-paniculate, sometimes pyramidal, the ultimate branches 3–7 mm long, minutely puberulous; receptacle glabrous. *Heads* ca. 8 mm high with 22–32 florets; the base of the involucre with 1–3 small linear-lanceolate bracts; involucral bracts ca. 23, subimbricate, in ca. 3 series, ovate to oblong with short-acute tips, the outer surface with 2–4 indistinct costae, minutely puberulous, often with glandular punctations; corolla lavender, 4–5 mm long, hairs usually mostly on outer surface of lobes, the lobes about as long as broad. *Achenes* 1.5–2.0 mm long, glabrous; pappus of 30–40 bristles mostly in 1 series, distal halves of the bristles often as wide or wider than the base.

As presently delimited, the species is known only from Costa Rica and Panama.

CHIRIQUÍ: Slopes of Las Cumbres near Cerro Punta, *Croat 13724* (MO). Bajo Chorro, Boquete, 6500 ft. *Davidson 266* (F, GH, MO, US).

16. BRICKELLIA

Brickellia Elliott, Sketch Bot. South Carolina and Georgia 2: 290. 1824 (1822), nom. cons. TYPE: *B. cordifolia* Elliott.

Kuhnia L., Sp. Pl., ed. 2. 1662. 1763. TYPE: *K. eupatorioides* L.
Coleosanthus Cass., Bull. Soc. Philom. 1817: 76. 1817. TYPE: *C. cavanillesii* Cass.
Rosalesia La Llave & Lexarza, Nov. Veg. Desc. 1: 14. 1824. TYPE: *R. glandulosa* La Llave *in* La Llave & Lexarza = *Brickellia cavanillesii* (Cass.) A. Gray.
Clavigera DC., Prodr. 5: 127. 1836. TYPE: *C. corymbosa* DC.
Bulbostylis DC., Prodr. 5: 138. 1836. TYPE: *Coleosanthus cavanillesii* Cass.
Ismaria Raf., Sylva Tell. 117. 1838. TYPE: *I. glandulosa* Raf.

Small to robust usually erect perennial *herbs* or *subshrubs*. *Leaves* opposite to alternate, sessile to petiolate; blades linear to broadly ovate, rarely trilobate, the margins subentire to coarsely serrate, teeth sometimes spiculiferous. *Inflorescence* paniculate to corymbose or racemose, rarely monocephalic. *Heads* discoid with 4–62 florets; involucre of 20–50 obtuse to long-acute subimbricate bracts, in 3–5 series; receptacle glabrous, usually flat; corolla narrowly tubular, usually constricted above, the lobes usually oblong-ovate, smooth, outer surface usually with glands, the cells of the corolla narrow with sinuous walls; anther collar with mostly oblong cells and with prominent annular thickenings, the exothecial cells subquadrate or wider than long, the anther appendage longer than wide, mostly oblong-ovate; style base with distinct enlarged node and dense contorted pubescence, the style appendage usually with very elongate thickened tips (slender in one species). *Achenes* prismatic with ca. 10 ribs, few to many bristles mostly between the ribs; carpopodium distinct, slightly to distinctly asymmetric, the cells small, mostly quadrate; pappus of 15–40 bristles, with flattened outer surface and scabrous to plumose lateral margins.

Brickellia contains about 100 species ranging from the southern United States to Mexico, Central America, and South America. The great majority of the species

are Mexican with only one species, *B. diffusa*, occurring in Panama and South America.

Literature:

Robinson, B. L. 1917. A monograph of the genus *Brickellia*. Mem. Gray Herb. 1: 3–151.

1. **Brickellia diffusa** (Vahl) A. Gray, Pl. Wright. 1: 86. 1852.—FIG. 17.

Eupatorium diffusum Vahl, Symb. Bot. 3: 94. 1794. TYPE: South America, *Forsskål* (C, not seen).
Bulbostylis diffusa (Vahl) DC., Prodr. 7: 268. 1838.
Eupatorium trichosanthum A. Rich. in R. de la Sagra, Fl. Cub., Fanerog. 3: 41. 1853. TYPE: Cuba, Jagua, *Ossa* (P, not seen).
Coleosanthus diffusus (Vahl) Kuntze, Rev. Gen. Pl. 1: 328. 1891.

Erect sparingly branched annual *herb* to 2 m tall; stems yellowish to slightly reddish, terete, scarcely striate, glabrous. *Leaves* opposite; blades deltoid to broadly ovate, to 10 cm long and 11 cm wide, the base broadly rounded to truncate, prominently acuminate and trinervate, the margins closely serrate-dentate, the apex shortly and abruptly apiculate, the upper surface with sparse short coarse pubescence, the lower surface densely covered with numerous oblong or reniform glands; petioles slender, to 6 cm long. *Inflorescence* a lax profusely branching elongate panicle with paniculate branches, the ultimate branches 4–20 mm long, glabrous. *Heads* ca. 7 mm high, slender, with mostly 8–14 florets; involucral bracts ca. 20, subimbricate, in 3–4 series, lanceolate to linear-lanceolate, 1–7 mm long, the apex sharply acute, the margins scarious, the outer surface bicostate, glabrous; corolla whitish, 4–5 mm long, slender, narrower above, glabrous except for a few glands on the lobes, the lobes minute; style branches filiform, tapering to the tip. *Achenes* 1.5–2.0 mm long, densely covered with small bristles; carpopodium prominent; pappus of 30–40 bristles with minutely scabrellous margins. *Pollen* mostly 20–25 μ in diameter, micropapillose.

The species is both the most widely distributed and most atypical member of the genus *Brickellia*. The genus is mostly restricted to the western United States, Mexico, and Central America, but *B. diffusa* occurs in Mexico southward to Peru and Brazil and also in the Greater Antilles. The genus and its relatives are generally characterized by the very broadly clavate style branches, but *B. diffusa* has filiform style branches with stigmatic lines sometimes reaching very near the tip. The species does retain most of the characteristic features of *Brickellia* including the appressed involucral bracts, the constricted corolla, the large and prominently tomentose style node, the ten-ribbed achene, and the flattened outer surfaces of the pappus bristles.

CANAL ZONE: Chiva-Chiva trail, Red tank to Pueblo Nuevo, *Piper 5741* (US). Balboa, *Standley 29298* (US). CHIRIQUÍ: Distrito Guanábano, Quebrada Guanabáno, 0–100 m, *Croat 22502* (MO). Quebrada Merida, 4 mi S of Puerto Armuelles, 0–100 m, *Liesner 383* (MO). Monte Verde, 2.5 km W of Puerto Armuelles, 80 m, *Liesner 59* (MO). DARIÉN: Isla Pedro Gonzales, *Duke 10396* (MO, OS). Above Paca, *R. S. Williams 710* (US). PANAMÁ: Juan Díaz, *Standley 30631* (US). Nuevo San Francisco, *Standley 30717* (MO, US).

A
H
B
C
D
F
G
E

17. CHROMOLAENA

Chromolaena DC., Prodr. 5: 133. 1836. TYPE: *C. horminoides* DC.

Heterolaena Schultz-Bip. ex Benth. & Hook., Gen. Pl. 2: 245. 1873. TYPE: *Eupatorium odoratum* L.

Osmia Schultz-Bip., Pollichia 22–24: 251. 1866. TYPE: *Eupatorium odoratum* L.

Eupatorium sect. *Cylindrocephala* DC., Prod. 5: 141. 1836. TYPE, present designation: *E. odoratum* L. = *Chromolaena odorata* (L.) R. M. King & H. Robinson.

Sparingly to densely branched *herbs* or *shrubs*. *Leaves* opposite; blades triangular to elliptical, the margins subentire to highly lobed. *Inflorescence* laxly to densely corymbose. *Heads* discoid with 10–45 florets; involucre of 18–45 ovate to lanceolate densely imbricate very unequal bracts, in 4–6 series, the bracts all deciduous at maturity; receptacle elongate, the upper surface flat to slightly convex, glabrous, paleae sometimes present; corolla tubular to narrowly funnelform with a scarcely constricted base, the outer surface mostly smooth with few to many short-stalked glands and often with rather stiff hairs, without stomates, the tips of the lobes usually capped with a group of thick-walled often prominently projecting cells, the inner surface of the lobes usually papillose with densely projecting cells, the cells inside corolla throat narrow with sinuous walls, with upper ends sometimes projecting; anther collar with numerous quadrate cells below, elongate cells above, usually with prominent ornate banding on walls, bands transverse in elongate cells and oblique or vertical in many shorter cells, the exothecial cells mostly about as long as wide, the anther appendage longer than wide, entire or toothed at the tip; style base not enlarged, glabrous, the surface cells of style appendages smooth to long-projecting. *Achenes* prismatic, 5-or rarely 3-ribbed, with bristles mostly on the ribs, sometimes with glands; carpopodium short-cylindrical, rarely narrowed below, the cells small, often wider than high with usually thickened walls; pappus of ca. 40 slender scabrous persistent bristles, the apical cells usually pointed. *Pollen* spinose, modified "type II" present in many species.

Chromolaena is a large and complex genus of more than 130 species. The greatest concentration of species is in Brazil where most of the closely related genera occur. Only the three most widely distributed species are found in Panama.

Literature:

King, R. M. & H. Robinson. 1970. Studies in the Eupatorieae (Compositae). XXIX. The genus *Chromolaena*. Phytologia 20: 196–209.

a. Inner involucral bracts with highly differentiated, expanded, often lavender-colored tips; leaves lanceolate to linear ..... 1. *C. ivaefolia*

aa. Inner involucral bracts with differentiated tips; leaves ovate to broadly elliptical.

←

FIGURE 17. *Brickellia diffusa* (Vahl) A. Gray.—A. Habit (× 3/5).—B. Heads (× 2 1/5).—C. Receptacle (× 8 9/10).—D. Achene cross section (× 16 7/10).—E. Florets (× 5 3/5).—F. Stamens (× 13 9/10).—G. Style with bases of branches (× 5 3/5).—H. Pappus bristle (× 11 1/10). [After Martius, Flora Brasiliensis 6(2): plate 102. 1876.]

b. Leaf blades deltoid to rhombic-ovate with prominent petioles, the lower surface with numerous red glands ..... 3. *C. odorata*
bb. Leaf blades broadly elliptical with short petioles, glabrous ..... 2. *C. laevigata*

1. **Chromolaena ivaefolia** (L.) R. M. King & H. Robinson, Phytologia 20: 202. 1970.

Eupatorium ivaefolium L., Syst. Nat., ed. 10. 2: 1205. 1759. TYPE: Jamaica, cultivated, *Swartz*? (LINN = 978.28, not seen, US, microfiche).
Osmia ivaefolia (L.) Schultz-Bip., Pollichia 22–24: 250. 1866.

Small *shrubs* or woody *herbs* to ½ m tall, unbranched; stems reddish-brown, terete, pubescent. *Leaves* opposite; blades narrowly elliptical, to 6 cm long and 2 cm wide, the base narrowly cuneate, the margins nearly entire, the apex narrowly acute to acuminate, the surfaces pubescent, the venation trinervate from near the base, the veins often prominent; petioles 1–5 mm long. *Inflorescence* a corymbose-panicle, sometimes multistratose, to 10 cm tall, the ultimate branches pubescent. *Heads* ca. 8 mm high with ca. 25 florets; involucral bracts ca. 30, imbricate, with 4–5 costae, the upper portions pubescent, the outer bracts oblong with rounded apices, the inner bracts with expanded and rounded usually lavender apices; receptacle naked; corolla violet, tubular, ca. 4 mm long. *Achenes* ca. 2 mm long, prismatic, 4–5-ribbed, the ribs bearing many short bristles; pappus of ca. 30 scabrous bristles, ca. 4.5 mm long, the apical cells acute.

Chromolaena ivaefolia ranges from the United States in the north through the West Indies and Mexico to Argentina and Bolivia in the south. The colored tips of the involucral bracts are distinctive.

CHIRIQUÍ: Pastures around El Boquete, 1000–1300 m, *Pittier 2903* (US). Llanos Francia, 3300 ft, *Stern et al. 1176* (MO).

2. **Chromolaena laevigata** (Lam.) R. M. King & H. Robinson, Phytologia 20: 202. 1970.

Eupatorium laevigatum Lam., Encycl. Méth. 2: 408. 1788. TYPE: America, *J. Jussieu*, Jussieu Herb. no. 8394 (P, not seen, US, microfiche).
E. psiadiaefolium DC., Prodr. 5: 144. 1836. TYPE: Brasil, in siccus ad Corcovado, *Lhostky* (G-DC, not seen, US, microfiche).

Shrubs or woody *herbs* to 2 m tall with few branches; stems reddish-brown, terete with slight striations, essentially glabrous. *Leaves* opposite; blades elliptical, to 10 cm long and 4 cm wide, the base cuneate to acuminate, the margins serrate to distal ½ to ⅔, the apex acute to short-acuminate, the surfaces glabrate, the venation trinervate from at or near the base, the veins prominent; petioles mostly 3–5 mm long. *Inflorescence* a corymbose panicle to 10 cm wide and 5 cm high, the ultimate branches 1–5 mm long, glabrous. *Heads* ca. 1 cm high with 15–20 florets; involucral bracts ca. 25–30, glabrate, imbricate, oblong, with 4–5 costae, the apex rounded; receptacle naked; corolla pale lavender, ca. 5 mm long, tubular. *Achenes* ca. 3.5 mm long, prismatic, 5-ribbed, the ribs with short bristles; pappus of ca. 25–30 scabrous bristles, ca. 5 mm long, the apical cells acute.

Chromolaena laevigata ranges widely from Mexico south to Argentina but is not known from the West Indies.

CHIRIQUÍ: Llanos del Volcán, ca. 1300 m, *Allen 1554* (F, MO, US). Vic. of Boquete, 3300–4200 ft, *Lewis et al. 621* (MO). Cerro Vaca, 900–1136 m, *Pittier 5300* (US). COCLÉ: El Valle de Antón, 600–800 m, *Allen 2861* (MO, US). PANAMÁ: Campana, 600–800 m, *Allen 1308* (F, MO, US). Cerro Campana, *Duke 6006* (MO); *Lewis et al. 3098, 3079* (both MO); *Tyson 6443* (FSU, MO). VERAGUAS: 1–2 mi above Santa Fé, *Gentry 3052* (MO).

3. **Chromolaena odorata** (L.) R. M. King & H. Robinson, Phytologia 20: 204. 1970.—FIG. 18.

Eupatorium odoratum L., Syst. Nat., ed. 10. 2: 1205. 1759. TYPE: Jamaica, Plukenet, Phytographia 177, *fig. 3.*
E. conyzoides Mill., Gard. Dict., ed. 8. 1768. (*Eupatorium* no. 14). TYPE: Jamaica, *Sloane*, cat. no. 124 (BM, not seen).
E. floribundum H.B.K., Nov. Gen. Sp. Pl. 4: 92. ed. fol. 1818. TYPE: "Peru", River Catamayo, Loxa, *Humboldt & Bonpland* (P, not seen, US, microfiche).
E. divergens Less., Linnaea 5: 138. 1830. TYPE: Mexico, near Hacienda de la Laguna, *Schiede & Deppe* (B, destroyed).
E. graciliflorum DC., Prodr. 5: 145. 1836. TYPE: Mexico, near Acapulco, *Haenke* (G-DC, not seen, US, microfiche).
Osmia odorata (L.) Schultz-Bip., Pollichia 22–24: 250. 1866.
O. divergens (Less.) Schultz-Bip., Pollichia 22–24: 252. 1866.
O. graciliflorum (DC.) Schultz-Bip., Pollichia 22–24: 252. 1866.
Eupatorium klattii Millsp., Publ. Field Columbian Mus., Bot. Ser. 2: 105. 1900. TYPE: Cuba, shore of Santiago Bay, *Millspaugh 1126* (F, not seen).

Woody *herbs* or reclining *shrubs* to 3 m tall, much branched; stems reddish-brown, terete, finely striate, glabrous to hirsute. *Leaves* opposite; blades deltoid to rhombic-ovate, to 9 cm long and 5 cm wide, the base cuneate to subtruncate, the margins entire to serrate, the apex narrowly acuminate, the upper surface glabrous, rarely pubescent, the lower surface with numerous short-stalked to sessile red glands, the venation prominently trinervate from near the base; petioles to 2 cm long. *Inflorescence* a broad panicle to 8 cm wide and 4 cm high with corymbose branches, the ultimate branches usually pubescent. *Heads* ca. 1 cm high with ca. 25 florets; involucral bracts ca. 15, glabrous to sparsely pubescent, imbricate, with 3–4 costae, the outer bracts oblong with rounded to truncate apices, the inner bracts narrow, short-acute; receptacle naked; corolla white, lavender, pink or light bluish, ca. 6 mm long, tubular. *Achenes* ca. 4 mm long, prismatic, 4–5-ribbed, ribs with short bristles; pappus of ca. 30 scabrous bristles, ca. 6 mm long, the apical cells acute.

Chromolaena odorata is widely distributed in the Americas from the southeastern United States south to Argentina. The species has been widely introduced into tropical parts of the Old World.

BOCAS DEL TORO: Bocas del Toro, *Carleton 173* (US). Almirante, *Cooper 130* (F). Banks of the Changuinola River, *Dunlap 416* (F). Peak behind waterfall on Quebrada N of Río Terebe ca. halfway between Quebrada Huron and Puerto Palenque, 400–800 ft, *Kirkbride & Duke 494* (MO). Changuinola to 5 mi S at junction of Ríos Changuinola and Terebe, 100–200 ft, *Lewis et al. 938* (MO). Water Valley, *von Wedel 864* (MO). Vic. of Chiriquí Lagoon, Water Valley, *von Wedel 1852* (MO, US). Vic. of Chiriquí Lagoon, Old Bank Island, *von Wedel 1861* (MO, US). CANAL ZONE: Vic. of Fort Clayton Test Center, *Blum 2052* (FSU, MO). Ancón, Cerro de Ancón, *Celestine 77* (US). Gamboa, *Heriberto 77* (US). Río Chagres, below the spillway of Gatún, *Busey & Mahler 340* (MO). Empire Range, *Correa & Gonzalez 519* (FSU). Barro Colorado Island, *Croat 4209* (MO), *4386* (F, MO), *4612, 6919, 7068, 7173, 7476, 7481* (all MO), *7789* (F, MO). 1 mi N of Summit Gardens, *Croat 12893* (F, MO). Barro Colorado Island, *Dressler 3426* (MO). Ancón Hill, *Greenman & Greenman 5107, 5128, 5140* (all MO). Between Summit and Gamboa, *Greenman & Greenman 5238* (MO). Road between Gamboa

FIGURE 18. *Chromolaena odorata* (L.) R. M. King & H. Robinson.—A. Habit (× ½).—B. Head (× 5⅔).—C. Achene (× 10⅘).—D. Style (×10⅘).—E. Corolla (× 10⅘).

and Summit Gardens, *Kennedy 2263* (MO). Balboa, *Macbride & Featherstone 25* (F, US). 1–3 mi from Gorgona, 40–150 m, *Maxon 4731* (US). Río Grande near Culebra, 50–100 m, *Pittier 2129* (US). Between Corozal and Ancón, 10–30 m, *Pittier 2205* (US). Barro Colorado Island, *Shattuck 686* (MO). Cerro Gordo, near Culebra, *Standley 26027* (US). Near Gatún, *Standley 27246* (US). Frijoles, *Standley 27614* (US). Gamboa, *Standley 28448* (US). Near

Fort Randolph, *Standley 28606* (US). Mount Hope Cemetery, *Standley 28787* (US). Old Las Cruces trail, between Fort Clayton and Corozal, *Standley 29146* (US). Las Cascadas Plantation, near Summit, *Standley 29588* (US). Vic. of Summit, *Standley 30117* (US). Vic. of Fort Sherman, *Standley 31214* (US). Quebrada Melgada, 70–75 m, *Steyermark 17473* (MO). Farfan Beach area, *Tyson & Blum 2613* (FSU, MO). Curundu, *Tyson 6061* (FSU), *6468* (MO); *Tyson & Lazor 6061* (FSU). Barro Colorado Island, *Wetmore & Abbe 36, 146* (both F); *Woodworth & Vestal 348, 495* (both F, MO). CHIRIQUÍ: Quebrada Manzanillo, 9 km S by SW of Puerto Armuelles, *Busey 729* (MO). Quebrada del Medio, 2 km N of Punta de Burica, 40–80 m, *Busey 749* (MO). 1 mi W of airport at Puerto Armuelles, near sea level, *Croat 21888* (MO). 4 km N of Burica, *McCorkle c-139* (FSU). Vic. of San Felix, 0–120 m, *Pittier 5199* (US). Cerro Vaca, 900–1136 m, *Pittier 5302* (US). COCLÉ: Vic. of El Valle, 800–1000 m, *Allen 81* (MO). Río Hato airstrip, *Burch et al. 1147* (MO). 3 mi NE of Antón, *D'Arcy 4104* (MO). 2.5 mi S of El Valle, 680–700 m, *McDaniel 8236* (FSU). Aguadulce, vic. of Puerto Aguadulce, *McDaniel & Cooke 14808* (FSU). COLÓN: East Santa Rita Ridge, *Correa & Dressler 608* (MO, US), *613* (FSU, MO, US), *649* (MO). Miguel de La Borda, *Croat 10040* (F, MO). East Santa Rita Ridge, *Dwyer 8402, 9339, 9354* (all MO). DARIÉN: Boca Grande tide gage, 50 ft, *Duke 1554* (OS, REED). Ca. 6 mi upstream from Morti Abajo, 100 m, *Duke 10156* (MO, REED), Isla Taboga, *Duke 10358* (MO). Isla Casaya, *Duke 10381* (MO). Isla Pedro Gonzales, *Duke 10398* (MO). Isla Espiritu Santo, *Duke 10452* (MO). Corredo, *Duke 15205* (REED). Near helipad at Hydro Camp on Río Morti, 229 ft, *Duke 15406* (FSU, MO). Río Sabana, *Roi Leopold III 223* (MO). HERRERA: Road from La Avena to Pesé, ca. 200 ft, *Burch et al. 1318* (F, MO). Between El Potrero and Las Minas, *D'Arcy 4137* (MO). 10 mi S of Ocú, *Tyson & Blum 2805* (FSU, MO). LOS SANTOS: 3 mi S of Carreta, *Burch et al. 1235* (US). Vic. of Bella Vista, *Piper 5321, 5342, 5388* (all US). PANAMÁ: Isla Taboga, 0–350 m, *Allen 1293* (F, MO). Cerro Jefe, 10–13 mi S of Goofy Lake, *Duke 8020* (OS). Isla del Rey, *Duke 9545* (MO). San José Island, *Duke 12509* (MO, OS). Goofy Lake to ca. 8 mi S of Goofy Lake, *Dwyer 7061* (MO). Chagres, *Fendler 1850* (MO). Chimán, *Lewis et al. 3334* (MO). Vic. of Panamá, *Macbride 2610, 2617* (both F, US). Pearl Islands, Saboga Island, *Miller 1978* (US). Bella Vista, *Standley 25313* (US). Las Sabanas, *Standley 25873* (US). Near Punta Paitilla, *Standley 26285* (US). Corozal Road, near Panamá, *Standley 26808* (US). Tobaga Island, *Standley 27102* (US). Vic. of Juan Franco Race Track, near Panamá, *Standley 27675* (US). Tobaga Island, *Standley 27852* (US). Río Tapia, *Standley 28054, 28215* (both US). Saboga Island, Pearl Islands, *Tyson & Loftin 5127* (FSU). SAN BLAS: Sasardi, ca. 20 m, *Duke 10146* (MO, OS). VERAGUAS: Hills W of Soná, ca. 500 m, *Allen 1046* (MO). 3.9–5 mi N of Santa Fé, *Gentry 3007* (MO). Puerto Mutis, 12 mi S of Santiago, *Tyson 6030* (FSU). La Mesa, *Tyson 6069* (FSU, MO).

18. CONDYLIDIUM

Condylidium R. M. King & H. Robinson, Phytologia 24: 380. 1972. TYPE: *Eupatorium iresinoides* H.B.K.

Perennial *herbs* or *subshrubs*, erect to decumbent, laxly branching. *Leaves* opposite; blades ovate, the base rounded to truncate, abruptly and narrowly decurrent into the petiole wing, the margins bluntly serrate to subentire, the apex short-acuminate; petioles distinct, short, winged to near the base. *Inflorescence* with laxly cymose and widely divergent branches. *Heads* discoid with 5–6 florets; involucral bracts 15 in 5 ranks, subimbricate, in 3 progressively longer series, widely spreading at maturity; receptacle glabrous, flat to slightly convex; corolla with a short distinct tube, the limb narrowly campanulate, the lobes slightly longer than wide, often with glands on outer surface, the margin often with a few short hairs, the corolla cells elongate with sinuous walls; anthers with lower part of filament short, the anther collar nearly as long as lower filament, the cells of the collar mostly subquadrate with only slight ornate thickening on the walls, the anther appendage slightly longer than wide; style base enlarged and densely short-hirsute, the style appendage linear and densely covered with elongate

papillae. *Achenes* prismatic with 5 ribs bearing numerous short bristles; carpopodium contorted and tapering with a sigmoid vascular trace, the smaller subquadrate thick-walled cells below, the upper cells more elongate; pappus with 30–40 slender scabrellous bristles in one series, persistent, the apical cells pointed. *Pollen* with short spines.

Condylidium contains two closely related species with one widely distributed in Central America, the West Indies and South America.

Literature:

King, R. M. & H. Robinson. 1972. Studies in the Eupatorieae (Asteraceae). CII. A new genus, *Condylidium*. Phytologia 24: 380–381.

1. **Condylidium iresinoides** (H.B.K.) R. M. King & H. Robinson, Phytologia 24: 381. 1972.—FIG. 19.

Eupatorium iresinoides H.B.K., Nov. Gen. Sp. Pl. 4: 83. ed. fol. 1818. TYPE: Colombia, near Ibague, *Humboldt & Bonpland* (P, not seen, US, microfiche).
E. glumaceum DC., Prodr. 5: 181. 1836. TYPE: Cuba, Havana, *Ossa* (G-DC, not seen, US, microfiche).
F. wageneri Hieron., Bot. Jahrb. Syst. 40: 375. 1908. TYPE: Venezuela, without locality, *Wagener 178* (B, destroyed, US, photo).
E. macrum Standley & Steyerm., Publ. Field. Mus. Nat. Hist., Bot. Ser. 23: 184. 1944. TYPE: Guatemala, Chiquimula, near Jocotán *Steyermark 31534* (F).

Erect sparingly branched perennial *herbs* or *subshrubs* to 2 m tall; stems mostly yellowish, terete, scarcely striate, hirtellous. *Leaves* opposite; blades ovate to ovate-lanceolate, to 11 cm long and 5 cm wide, the base rounded to cuneate, rather abruptly decurrent at petiole, the margins subentire to serrate-dentate, the apex somewhat narrowly acuminate, the upper surface sparsely puberulous, the lower surface densely puberulous to tomentellous, with glandular punctations, the veins prominently trinervate from near base; petioles to 2.5 cm long, becoming narrowly winged distally. *Inflorescence* a lax panicle with laxly cymose branches, the branching divaricate, often appearing regularly dichotomous, the branches densely hirtellous; heads in small clusters of 3–6 with ultimate branches of inflorescence to 3 mm long. *Heads* 4–5 mm high with 5–6 florets; involucral bracts 15, subimbricate, in 5 ranks and 3 series, 0.5–3.5 mm long, suborbicular to narrowly lanceolate, 2–4 costate, mostly glabrous with slightly puberulous tips, the margins scarious, the acute tips often with minute apicules; corolla white, 2.5–3.5 mm long, the tube distinct, 1.0–1.5 mm long; the limb narrowly campanulate, the lobes about as long as wide, with glands and usually a few short submarginal hairs on outer surface. *Achenes* 1.5–2.0 mm long with sparse short scattered bristles; carpopodium very prominent on one side; pappus of ca. 30 bristles, mostly 2.5–3.5 mm long. *Pollen* 18–20 μ in diameter.

Condylidium iresinoides is widely distributed, occurring from Guatemala to Venezuela and southward along the Andes to Bolivia with records from the Lesser Antilles and Cuba. The species can usually be distinguished by the rather regularly dichotomous appearance of the branches of the inflorescence. The five-ranked involucral bracts are particularly evident in older, spreading involucres.

FIGURE 19. *Condylidium iresinoides* (H.B.K.) R. M. King & H. Robinson.—A. Habit (× 2/5).—B. Head (× 7⅕).—C. Corolla (× 22).—D. Style (× 17).—E. Achene (× 22).

CANAL ZONE: Near the sea beneath Thatcher Bridge, *D'Arcy & D'Arcy 6084* (MO). Near beach at Fort Kobbe, *Duke 4224* (MO, US). COCLÉ: Vic. of El Valle, 600–1000 m, *Allen 1167* (F, MO, US). Hills S of El Valle de Antón, 600–800 m, *Allen 2862* (MO, US). 3 mi NE of Antón, *Croat 9628* (MO). El Valle, *Ebinger 1102* (MO, US). 8 mi SE of Antón, *King 5270* (US). W slopes of El Valle, *King 5322* (US). Llano Bonito, N of Las Margaritas, 400–500 m, *Seibert 518* (MO, US). DARIÉN: Río Cucunati at Puente Quemado, *Duke 8814* (OS). PANAMÁ: Taboga Island, 300 m, *Allen 116* (MO). Hills above Campana, 600–800 m, *Allen 1305* (F, MO). Cerro Campana, *Croat 12025* (MO). Morro Island, *D'Arcy & D'Arcy 6783* (MO). Interam. Hwy. 4 mi NW of Bejuco, *Duke 4564* (MO, US). Cerro Campana, *Duke 5969* (MO), *8673* (MO, OS, US). Road from Pan-Am. Hwy. to Coronado Hwy., *Duke 11795* (MO, US). Taboga Island, *Dwyer 2810* (MO, US). La Campana, Cerro Campana, *Ebinger 926* (MO). Taboga Island, near sea level, *Gentry 5729* (MO). E of Chica, *King 5263* (US). Taboga Island, *Standley 27016, 27850* (both US). W slope of Cerro Campana, 2500 ft, *Tyson et al. 2394* (MO, US). Isla Taboga, ca. 0–186 m, *Woodson et al. 1479* (MO, US). SAN BLAS: Hills SE of Puerto Obaldia, *Croat 16740* (MO).

19. CRITONIA

Critonia P. Browne, Civ. Nat. Hist. Jam. 490. 1756. TYPE: *Eupatorium dalea* L.

Wikstroemia Spreng., Kongl. Vetensk. Acad. Handl. 1821: 167. 1821; not *Wikstroemia* Schrad. (Theaceae), nom. rej.; nor *Wikstroemia* Endlich. (Thymelaeaceae), nom. cons. TYPE: *W. glandulosa* Spreng. = *Critonia dalea* (L.) DC.

Very coarse perennial *herbs* to small *trees* or woody *vines*, sparingly branched; stems often fistulose. *Leaves* opposite, distinctly petiolate; blades elliptical to broadly ovate, the base cuneate to subtruncate or hastate, without glandular punctations, internally with distinct lacticifers beside the veins or in centers of areoles; petioles sometimes winged. *Inflorescence* paniculate, the branches opposite and usually spreading at 90° angles. *Heads* discoid with 4–12 florets, usually sessile or short stalked in clusters of 2–12; involucral bracts ca. 20–25, imbricate to subimbricate, in 4–6 series, stramineous, usually glabrous and striate, the outer series short-ovate to orbicular, persistent, the inner series elliptical to narrowly oblong, easily deciduous; receptacle flat to slightly convex, glabrous; corolla narrowly funnelform, glabrous, rarely a few glands on the lobes, the lobes 5, narrowly oblong to long-triangular, smooth, the corolla cells elongate with slightly sinuous walls; anther filament short, inserted above lower third of corolla, the anther collars slender, usually with distinct quadrate cells with cell walls inornate or with slight annular thickenings, the exothecial cells mostly subquadrate, the anther appendages large, usually longer than wide; style base without enlargement, glabrous, the style appendages filiform to narrowly spathulate, smooth to slightly mamillose. *Achenes* prismatic with 5 often prominent ribs, with or without bristles; carpopodium a narrow rim or short cylinder, the cells small, quadrate to rounded, the cell walls with confluent thickenings; pappus of 25–35 scabrous coarse persistent bristles with crowded bases, the tips slightly enlarged and more closely scabrous, the apical cells usually acute.

Critonia contains about 33 species ranging from Mexico to Central America, the West Indies, and South America. Most of the species are found in Central America and the West Indies. Three species are known from Panama. The lacticifers of the leaves, although completely included in the leaf tissue, are sometimes very prominent and easily seen in living material.

Literature:

King, R. M. & H. Robinson. 1971. Studies in the Eupatorieae (Asteraceae). XLVIII. The genus *Critonia*. Phytologia 22: 46–51.

a. Heads with 5 florets; leaf blades narrowly elliptical with prominent lacticifers in areoles; lower secondary veins short, not parallel to the leaf margin; achenes with very small carpopodium; pappus bristles 25–30 ..... 2. *C. daleoides*
aa. Heads with 8–12 florets; leaf blades usually ovate with lacticifers not prominent in areoles; lower secondary veins long, parallel to the leaf margin; achenes with broad carpopodium; pappus bristles 35–40.
  b. Vines; mature heads mostly 1.0–1.2 cm high; pappus bristles in 1–2 series with sharply angled bases, the tips distinctly broadened ..... 1. *C. billbergiana*
  bb. Usually shrubs or small trees; heads mostly 0.8–1.0 cm high; pappus bristles in 1 series with terete bases, the tips not or only slightly broadened ..... 3. *C. morifolia*

1. **Critonia billbergiana** (Beurl.) R. M. King & H. Robinson, Phytologia 22: 48. 1971.—Fig. 20.

Eupatorium billbergianum Beurl., Kongl. Svenska Vetenskapsakad. Handl. 1854: 134. 1856. TYPE: Panama, near Porto Bello, *Billberg 300* (S).

Sparsely branching woody *vines*; stems greenish to pale brownish, terete, scarcely striate, glabrous. *Leaves* opposite; blades ovate, to 11 cm long and 5 cm wide, the base cuneate to somewhat rounded, parallel to the long basal secondary veins, the margins remotely serrulate to subentire, the apex slightly short-acuminate, the surface usually glabrous, sometimes sparsely pilose below on veins, the venation subpinnate to trinervate, the second pair of secondary veins most prominent; petioles to 2 cm long. *Inflorescence* pyramidally paniculate with the lowest branches in the axils of normal leaves, the branches densely corymbose with branchlets bearing few heads, glabrous to puberulous, the ultimate branches 0–4 mm long. *Heads* 9–12 mm high with 8–9 florets; involucral bracts 20–25, imbricate to subimbricate, in 4–5 series, 1–6 mm long and 1.5 mm wide, ovate to oblong-lanceolate with narrowly rounded apex, the innermost bracts acute, coriaceous, the outer surface glabrous; corolla whitish, 5–7 mm long, tubular or with a narrowly funnelform limb, glabrous, the lobes ca. 0.5 mm long, narrowly triangular; style branches slightly broadened distally. *Achenes* 3–4 mm long with 5–6 narrow ribs, numerous hairs on upper part, glabrous below, the achene base scarcely narrowed with broad carpopodium; pappus of ca. 40 crowded bristles partially in second series, 5–7 mm long, the bases of the bristles with distinct margins and flattened outer surfaces, the tips slightly but distinctly enlarged.

Critonia billbergiana is known from British Honduras, Guatemala, Honduras, Costa Rica, and Panama. The plants seem to be strictly vines and have less branched inflorescences and distinctly larger heads than either of the other Panamanian species.

BOCAS DEL TORO: Water Valley, vic. of Chiriquí Lagoon, *von Wedel 1817* (MO). CANAL ZONE: Chagres, *Fendler 154* (MO). Cerro Galera, 350–400 m, *Gentry 6622* (MO). Pipeline road 5–6 mi N of Gamboa, *Gentry 6672* (MO). COLÓN: Portobelo, *Billberg 300* (S). PANAMÁ: Cerro Azul, *Dwyer 3071* (MO). Cerro Campana, *Dwyer et al. 4714* (MO). Madden Lake, *Gentry & Tyson 5033* (MO). 2–3 mi S of Goofy Lake, 2000–2200 ft, *Lewis et al. 265, 285* (both MO). SAN BLAS: Isla Soskatupa, *Duke 8944* (MO, REED).

FIGURE 20. *Critonia billbergiana* (Beurl.) R. M. King & H. Robinson.—A. Habit (× ½).—B. Head (× 5).—C. Corolla (× 12½).

2. **Critonia daleoides** DC., Prodr. 5: 141. 1836. TYPE: Mexico, Tampico, Tamaulipas, *Berlandier* 1827 (G-DC, not seen, US, microfiche).

Eupatorium daleoides (DC.) Hemsl., Biol. Cent. Amer., Bot. 2: 94. 1881.

Shrubs to 8 m tall, with few to many branches; stems dark near tips, becoming pale in older parts, terete to slightly hexagonal, slightly striate, glabrous to very sparsely pilose. *Leaves* opposite; blades narrowly elliptical, to 23 cm long and 5 cm wide, the base narrowly cuneate with short spreading secondary veins, the margins closely serrate, the apex narrowly acute to slightly acuminate, the surfaces glabrous, a few hairs on the veins below, the veins pinnate, the lacticifers in the areoles prominent; petioles short, 0.5–1.5 cm long. *Inflorescence* pyramidally paniculate with densely corymbose branches, the branches puberulous or short-pilose, the ultimate branches 0.1 mm long. *Heads* 6–7 mm high with 5 florets; involucral bracts ca. 20, imbricate to subimbricate, in 4–5 series, 1–5 mm long, to 1.5 mm wide, ovate to oblong-elliptical with rounded apex, papyraceous with usually 4 slender costae, glabrous on outer surface; corolla white, 4.0–4.5 mm long, broadly tubular with narrowly funnelform limb, glabrous, the lobes 0.5–0.7 mm long, twice as long as wide; style branches slightly broadened distally. *Achenes* ca. 2.5 mm long, with broad pale ribs, densely setiferous, the achene base very narrow with minute carpopodium; pappus of ca. 25–30 slender bristles, 3–4 mm long, the tips slightly but distinctly broadened.

Critonia daleoides is distributed throughout Central America and extends north into central Mexico The species is a member of the typical element of the genus which is otherwise restricted to the West Indies. The characters in common with the West Indian relatives are the more prominent lacticifers in the leaves, the smaller number of florets per head, and the broader ribs and smaller carpopodium of the achene.

CHIRIQUÍ: Paso Ancho to Monte Lirio, upper valley of Río Chiriquí Viejo, 1500–2000 m, *Allen 1489* (F, MO). 5.5 mi S of Cerro Punta, 1700 m, *Graham 272* (MICH). Vic. of El Boquete, 990 m, *Maurice 753* (US). Vic. of El Boquete, 1000–1300 m, *Maxon 5150* (US). 0.5 mi N of El Hato del Volcán, 1350 m, *McDaniel 10069* (FSU). Cerro Vaca, 900–1136 m, *Pittier 5296* (US). Vic. of Boquete, 3500 ft, *Stern et al. 1941* (MICH, MO). COCLÉ: Vic. of El Valle, 800–1000 m, *Allen 75* (MO, US). Vic. of El Valle, 600–1000 m, *Allen 1173* (F, MO). Hill S of El Valle de Antón, 600–800 m, *Allen 2851* (MO, US). El Valle, *Harvey 5167* (F). 2 mi S of El Valle, 600 m, *McDaniel 8247* (FSU, US).

3. **Critonia morifolia** (Miller) R. M. King & H. Robinson, Phytologia 22: 49. 1971.

Eupatorium morifolium Miller, Gard. Dict., ed. 8. 1768. (*Eupatorium* no. 10). TYPE: America, *Houston* (BM?, not seen).
E. populifolium H.B.K., Nov. Gen. Sp. Pl. 4: 87. ed. fol. 1818. TYPE: Mexico, near Mazatlan, *Humboldt & Bonpland* (P, not seen, US, microfiche).
E. critonioides Steetz in Seem., Bot. Voy. Herald 145. 1853. SYNTYPES: Panama, Volcán Chiriquí, *Seemann*. Panama, Veraguas, *Seemann* (both BM, not seen).
E. megaphyllum Baker in Mart., Fl. Bras. 6(2): 322. 1876. TYPE: Brazil, Caldas, Minas Geraes, *Regnell 692* (S, lectotype, not seen; B, isolectotype, destroyed, US, photo).
E. sartorii Schultz-Bip. ex Klatt, Leopoldina 20: 91. 1884, nom. nud. pro syn.

Erect to subscandent *shrubs* or small *trees* to 6 m high, with few to many branches; stems pale-brownish, often paler in older parts, terete to slightly

hexagonal, distinctly striate, pubescence flocculose, becoming glabrous. *Leaves* opposite; blades ovate to broadly ovate, to 25 cm long and 15 cm wide, the base cuneate to truncate, parallel to the long basal secondary veins, the margins usually closely serrate to crenulate, the apex slightly to sharply short-acuminate, the surfaces with sparse weak puberulence, becoming glabrous, flocculose below on veins, the venation subpinnate with 2 pairs of secondary veins in the basal ⅙, the second pair usually more ascending; petioles to 8 cm long. *Inflorescence* pyramidally paniculate with densely corymbose branches and branchlets, the branches puberulous to flocculose, the ultimate branches 0–2 mm long. *Heads* 8–10 mm high with 8–12 florets; involucral bracts ca. 25–30, imbricate to subimbricate, in 5–6 series, 1–6 mm long and 1.0–1.5 mm wide, ovate to narrowly oblong, the apex rounded, the surface papyraceous to coriaceous with ca. 4 usually broad or indistinct costae, glabrous to finely puberulous; corolla whitish, 4–5 mm long, tubular, glabrous, the lobes ca. 0.5 mm long, narrowly oblong; style branches filiform, not broadened distally. *Achenes* 2.0–3.0 mm long, with narrow ribs, nearly glabrous to sparsely puberulous, the achene base slightly to greatly narrowed with a distinct broad carpopodium; pappus of 35–40 slender bristles, mostly 4.5–5.5 mm long, the bases not or scarcely angled, mostly terete, the tips not or scarcely broadened.

The species is widely distributed from Mexico through Central America and south to Argentina. A similar species, *Critonia sexangularis* (Klatt) R. M. King & H. Robinson, is reported from Guatemala south to Costa Rica but is not known from Panama. This latter species can be distinguished by its much more sharply angled stems.

BOCAS DEL TORO: Quebrada Huron, 300–400 ft, *Kirkbride & Duke 453A* (MO, REED). CANAL ZONE: 6 mi N of Gamboa, *Tyson 3488* (FSU). CHIRIQUÍ: Distrito Baru along ridge above Brazo Seco near Costa Rican Border, 100–200 m, *Croat 22555* (MO). Quebrada Melliza, 6 mi S of Puerto Armuelles, 0–150 m, *Liesner 462* (MO). Between Concepción and El Volcán, *White 313* (MO). COCLÉ: Road to La Mesa above El Valle, *Croat 14410* (MO). El Valle to La Mesa, 2000 ft, *Tyson et al. 3974* (MO). DARIÉN: Río Sambú between Sambú and Río Venado, *Duke 931A* (US). Manené, *Kirkbride & Bristan 1568* (MO).

20. DECACHAETA

Decachaeta DC., Prodr. 5: 133. 1836. TYPE: *D. haenkeana* DC.

Glandular pubescent to glabrous *shrubs* or *subshrubs*, sparingly branched. *Leaves* alternate (opposite in one species); blades elliptical to ovate or suborbicular, sometimes slightly lobed; petioles short to long. *Inflorescence* a many-headed thyrsoid panicle. *Heads* discoid with 4–30 florets; involucral bracts 10–15, in 3–4 series, imbricate, unequal, oblong or oblong-lanceolate to suborbicular, the apex rounded or obtuse to acutely pointed, the outer surface green to light yellow or brown, with 0–5 costae, pubescent, with either glabrous or ciliate margins; receptacle highly convex, with a dense tuft of hair; corolla narrowly tubular to narrowly funnelform, white, 5-lobed, glabrous or with glandular punctations, the lobes about as long as wide, composed of large thin-walled cells, smooth except at extreme tips on outer surface; anther collars long and narrow with mostly

subquadrate cells below, the cell walls thin, not ornamented, the exothecial cells quadrate, the anther appendage extremely short and broad with a reflexed margin; style base not enlarged, glabrous, the style branches only slightly broadened distally, mamillose. *Achenes* prismatic, 5-ribbed with bristles mostly on the ribs; carpopodium slightly to well developed, composed of 5–6 tiers of rather thick-walled cells; pappus of 10–30 slender deciduous bristles, somewhat to distinctly enlarged apically, scabrous or partly barbellate, the apical cells acute. *Pollen* minutely papillose.

Decachaeta contains seven species which are mostly found in Mexico and Guatemala. One species is found farther south in Costa Rica and Panama. The name of the genus is in reference to the reduced number of pappus bristles in the type species. Actually, all members of the genus have a somewhat reduced number of bristles for the tribe, averaging between 20 and 25. The type species tends to have the fewest bristles, usually 15–18, but there seems to be no justification for the generic name or the separate status long enjoyed on this basis. The lower counts are probably usually the result of loss of some of the fragile pappus bristles.

The form of the inflorescence, the reduced anther appendage, and the reduced spines on the pollen have led to the suggestion that species of *Decachaeta* and members of some related genera might be wind-pollinated (Grashoff & Beaman, 1970, see under *Koanophyllon*).

Literature:

King, R. M. & H. Robinson. 1969. Studies in the Eupatorieae (Compositae). XVI. A monograph of the genus *Decachaeta* DC. Brittonia 21: 275–284.

——— & ———. 1971. Studies in the Eupatorieae (Asteraceae). XXXVII. The genus *Hebeclinium*. Phytologia 21: 298–301.

1. **Decachaeta thieleana** (Klatt) R. M. King & H. Robinson, Brittonia 21: 281. 1969.—Fig. 21.

Eupatorium myriocephalum Klatt, Leopoldina 25: 104. 1889, not *Eupatorium myriocephalum* Gardn., 1847. TYPE: Costa Rica, Ojo de Agua, *Hoffmann* 389 (GH, isotype).

E. thieleanum Klatt, Bull. Soc. Roy. Bot. Belgique 31: 191. 1892 (1893). TYPE: Costa Rica, Taillis du Rodeo de Pacaca, 900 m, *Pittier 1603* (GH, lectotype).

E. myrianthum Klatt, Leopoldina, Bot. Beibl. 3: 1895. TYPE: Costa Rica, *Pittier 1603* (GH, lectotype).

Erect *herb* or *shrub* to 4 m tall, sparingly branched; the leaves, involucral bracts, corolla, and styles bearing short-stalked capitate glands; stems terete, faintly striate, brown. *Leaves* alternate; blades broadly ovate with a large dentation on each side, to 17 cm long and 15 cm wide, the lower leaves as much as 25 cm long and 24 cm wide, the margins serrate, the apex short-acuminate, the second or third pair of the secondary veins usually prominent and strongly ascending from near the basal fourth of blade; petioles 3–7 cm long, not winged. *Inflorescence* a thyrsoid panicle, to 25 cm long and 10 cm wide. *Heads* numerous, 5–6 mm high with ca. 25 florets; involucral bracts ca. 15, oblong-lanceolate, with a few costae, the apex usually obtusely pointed, pubescent;

FIGURE 21. *Decachaeta thieleana* (Klatt) R. M. King & H. Robinson.—A. Habit (× ⅖).—B. Head (× 5⅜10).—C. Corolla (× 13⅕).

receptacle highly convex, with a dense tuft of hairs; corolla white, 3.5 mm long, narrowly funnelform, the lobes broadly triangular, ca. 0.4 mm long and wide. *Achenes* ca. 1.8 mm long with some short bristles on the upper part; pappus of 25–30 bristles, ca. 3 mm long, the tips not dilated.

Decachaeta thieleana is known only from Costa Rica and Panama. The somewhat aceriform leaves are a useful distinction.

CHIRIQUÍ: Paso Ancho to Monte Lirio, 1500–2000 m, *Allen 1473* (F, MO, US). Lerida, 4400 ft, *Maurice 871* (US). Vic. of Nueva Suisa, *Croat 13506, 13788* (both MO). Bajo Chorro, 6000 ft, *Davidson 425* (F, MO). Florida State University Tropical Biology Station, 2.5 mi S of Cerro Punta, 5500 ft, *Kazlovsky K-3*, (MO). Vic. of El Boquete 1000–1300 m, *Maxon 4994* (US). Río Ladrillo and vic., 1200–1300 m, *Pittier 3057* (US). Chiriquí Viejo Valley, *White 97* (MO).

21. FLEISCHMANNIA

Fleischmannia Schultz-Bip., Flora 33: 417. 1850. TYPE: *F. rhodostyla* Schultz-Bip. = *F. arguta* (H.B.K.) B. L. Robinson.

Sparingly branched *herbs* or *subshrubs*. *Leaves* opposite, rarely subopposite or alternate; blades elliptical to rhomboidal or broadly cordate-ovate, the margins usually serrate or crenate, rarely serrulate (leaves dissected into long narrow segments in one species); petioles slender. *Inflorescence* laxly branching with laxly cymose to densely corymbose branches. *Heads* discoid with 10–50 florets; involucre of 20–30 narrow obtuse to acuminate subimbricate usually unequal bracts, in 2–4 series, spreading at maturity; receptacle usually glabrous, sometimes with minute scattered hairs, usually flat; corolla with a short basal tube, the limb narrowly funnelform, the outer surface above or on the lobes often with short hairs or glands, the lobes short, broadly triangular, with projecting cells on outer surface and along margins, the cells of much of the inner surface of lobes and limb with upper ends projecting as papillae, the cells of the limb mostly narrow with sinuous walls; anther collar usually slender, with elongate cells showing distinct transverse thickenings throughout, without distinct short cells below, the exothecial cells mostly quadrate or wider than long, the anther appendage broadly ovate or oblong; style without basal enlargement, glabrous, the cells of style appendage linear, densely long-projecting. *Achenes* prismatic, usually with bristles or scabrae on the ribs or upper surfaces, usually without glands; carpopodium distinct with prominent upper rim, rounded with thick-walled usually quadrate cells; pappus of 5–40 slender sometimes slightly fragile bristles, the apical cells pointed.

Fleischmannia contains about 70 known species ranging from the southeastern United States and Mexico through Central America and the West Indies to Argentina in South America. In South America the genus is concentrated in the Andes. One species, *F. microstemon*, has become adventive in West Africa. Eleven species are found in Panama.

The genus shows a superficial resemblance to some members of the genus *Ageratina* but the two are not closely related. Basic differences occur in many details of the corollas, the anther collars, the achenes, and the pappus. *Fleischmannia* is also cytologically distinct with base numbers of $x = 4$ and $x = 10$ (Baker, 1967).

Literature:

Baker, H. G. 1967. The evolution of weedy taxa in the *Eupatorium microstemon* species aggregate. Taxon 16: 293–300.

King, R. M. & H. Robinson. 1970. Studies in the Eupatorieae (Compositae). XVIII. New combinations in *Fleischmannia*. Phytologia 19: 201–207.

a. Leaves with primarily pinnate venation, the margin distinctly doubly crenate ---- 1. *F. allenii*
aa. Leaves prominently trinervate from the base, the margin simply crenate or serrate.
  b. Heads about 3 mm high; corollas about 2 mm long.
    c. Perennial; leaf tips acuminate; branches of inflorescence with heads in small corymbose clusters; involucral bracts rounded to short-acute ------- 4. *F. hymenophylla*
    cc. Annual; leaf tips acute; branches of inflorescence with heads in lax cymes; involucral bracts acute to narrowly long-acuminate.
      d. Leaves narrowly elliptic with narrowly cuneate bases ---------- 6. *F. misera*
      dd. Leaves rhomboid-ovate ---------- 10. *F. sinclairii*
  bb. Heads about 4–6 mm high; corollas usually 2.5–3.5 mm long.
    e. Leaves narrowly elliptic to linear-lanceolate with narrowly cuneate bases; receptacle slightly convex or conical ---------- 9. *F. sideritidis*
    ee. Leaves ovate to rhombic with short-cuneate to rounded or cordate bases; receptacle usually flat.
      f. Annual; achenes with ribs usually yellow to maturity; inflorescence often lax ---------- 5. *F. microstemon*
      ff. Perennial; achenes evenly darkening without persistently yellow ribs; inflorescence with compact corymbose branches.
        g. Leaves with broadly rounded or cordate bases, without glandular punctations.
          h. Erect shrubby herbs with densely pubescent leaves; stem leaves acute to scarcely acuminate; ribs of achenes bearing many short bristles ---------- 11. *F. tysonii*
          hh. Subscandent herbs with very sparsely pubescent leaves; stem leaves rather abruptly short-acuminate; ribs of achenes sparsely scabrous to glabrous ---------- 2. *F. chiriquensis*
        gg. Leaves with broadly cuneate to truncate bases, with glandular punctations.
          i. Inflorescence a broad flat-topped corymbose panicle; base of involucre abrupt with compact lower bracts ---------- 3. *F. croatii*
          ii. Inflorescence a series of rather compact glomerulate corymbose branches; base of involucre with loose lower bracts.
            j. Involucral bracts glabrous or with sparse appressed puberulence, lateral margins narrowly scarious; leaves glabrous below except on larger veins; heads with 20–25 florets; style branches thickened ---------- 7. *F. panamensis*
            jj. Involucral bracts prominently puberulent to pilose, lateral margins broadly scarious; leaves puberulous below; heads with 15–20 florets; style branches usually slender ---------- 8. *F. pratensis*

1. **Fleischmannia allenii** R. M. King & H. Robinson, Phytologia 28: 73. 1974. TYPE: Panama, vic. of "New Switzerland," Chiriquí, *Allen 1347* (MO, holotype; US, isotype).

Erect perennial coarse *herbs* or *subshrubs* to 1.5 m tall, rarely branching; stems greenish to brown with dense reddish puberulence, slightly ribbed. *Leaves* opposite; blades papyraceous, broadly elliptical, to 15 cm long and 9 cm wide, the base cuneate to narrowly acuminate, the margins distinctly bi- to tri-crenate, the apex acute to scarcely acuminate, the upper surface sparsely puberulous, the lower surface with glandular punctations, puberulous on veins, the venation mostly pinnate; petioles slender, to 5 cm long. *Inflorescence* a broad corymbose panicle with densely corymbose branches, the ultimate branches 2–4 mm long, densely puberulous. *Heads* ca. 5 mm high with 20–25 florets; involucral bracts ca. 28–30, subimbricate to imbricate, unequal, in 3–4 series, mostly 4-seriate,

short-acute with scarious margins, the outer surface puberulous, the inner bracts with more scarious tips; corolla lavender, ca. 3 mm long, with many sharp-pointed hairs above and on lobes; style branches slightly thickened. *Achenes* scarcely constricted above, black when mature with black ribs, glabrate to sparsely bristly above and on the ribs; pappus of ca. 30 scabrous contiguous bristles.

The species is apparently endemic to the Chiriquí region. *Fleischmannia allenii* has distinctive leaf venation and margins. The species may be closely related to *F. plectranthifolia* (Benth.) R. M. King & H. Robinson of Costa Rica but the latter has more rounded leaf bases and lacks glandular punctations. The corollas of *F. allenii* have hairs that are sharper and that cover more of the outer surface than in other related species.

CHIRIQUÍ: Vic. of 'New Switzerland,' central valley of Río Chiriquí Viejo, *Allen 1347* (MO). Vic. of Methodist Camp near Nueva Suissa, *Croat 13516* (MO). Hill N of Audobon Cabin, *Croat 13652* (MO). Ca. 2 mi W of Cerro Punta, 1630 m, (FSU). Bajo Mona, mouth of Quebrada Chiquero, along Río Caldera, 1500–2000 m, *Woodson et al. 1013* (MO).

2. **Fleischmannia chiriquensis** R. M. King & H. Robinson, Phytologia 28: 74. 1974. TYPE: Panama, Cerro Respinga, Chiriquí, *Gentry* 5928 (MO).

Flexuous perennial *herbs* or *vines* to 3 m tall; stems greenish to slightly reddish, terete, finely striate, weakly pilose to glabrescent. *Leaves* opposite; blades papyraceous, broadly ovate, to 6 cm long and 5 cm wide, the base broadly cordate, the margins closely and bluntly serrate-crenate, the apex abruptly short-acuminate, the surfaces sparsely pilose, puberulous on veins, without glandular punctations, the veins prominently trinervate from the base; petioles slender, to 2.5 cm long. *Inflorescence* a broad corymbose panicle with compact corymbose branches, the ultimate branches 2–4 mm long, densely puberulous. *Heads* ca. 5 mm high with 20–25 florets; involucral bracts ca. 20, subimbricate, unequal, in ca. 3 series, mostly bicostate, mostly short-acute with rather broad scarious margins, the outer surface pilose to sparsely puberulous, the inner bracts with more rounded more scarious usually minutely apiculate tips; corolla lavender, 3.0–3.5 mm long, with many short hairs on outer surface of lobes; style branches slightly thickened distally. *Achenes* slightly constricted above, black when mature with black ribs, sparsely scabrid or with short bristles on the ribs; pappus of 27–30 scabrous contiguous bristles.

Fleischmannia chiriquensis is known only from the Cerro Punta area of Chiriquí Province. The species is most closely related to *F. tysonii* of Volcán Chiriquí but it also superficially resembles *F. plectranthifolia* (Benth.) R. M. King & H. Robinson of Costa Rica. The latter species is distinguished by the more elongate, usually noncordate leaves having 5–7 veins prominently concentrated at the base. The inner involucral bracts of the latter species are also much more pointed and the achene ribs are sometimes yellow.

CHIRIQUÍ: Above Cerro Punta, 6300 ft, *D'Arcy* 5372 (MO). Slope of Respinga above town of Cerro Punta, 8400 ft, *D'Arcy & D'Arcy* 6545 (MO). Along Boquete trail, Cerro Respinga, E of town of Cerro Punta, ca. 2000–2500 m, *Gentry* 5928 (MO).

3. **Fleischmannia croatii** R. M. King & H. Robinson, Phytologia 28: 76. 1974. TYPE: Panama, vic. of Las Nubes, Chiriquí, *Croat 22400* (MO).

Erect perennial coarse *herbs* or *subshrubs* to 1.5 m tall; stems brownish-green, terete, finely striate, weakly but densely hirsute. *Leaves* opposite; blades papyraceous, ovate, to 7 cm long and 4.5 cm wide, the base subtruncate, the margins crenate-serrate, the apex shortly but distinctly acuminate, the upper surface sparsely pilose, the lower surface with glandular punctations, sparsely long-pilose mostly on veins, the veins prominently trinervate from the base; petioles slender, to 5 cm long. *Inflorescence* a broad dense flat-topped corymbose panicle with long ascending lateral branches, the ultimate branches 1–4 mm long, hirtellous. *Heads* ca. 6 mm high with ca. 20 florets; the base of the involucre abrupt with compact lower bracts; involucral bracts 20–25, subimbricate, unequal, in ca. 3 series, bicostate, mostly short-acute, the scarious margins narrow, the outer surface prominently puberulous; corolla lavender, 3.5–4.0 mm long, the lobes with many sharp hairs and a few glands on outer surface; style branches not thickened. *Achenes* only slightly constricted above, black when mature with black ribs, sparsely scabrid on the ribs; pappus of 25–30 scabrous contiguous bristles.

The species is in the series including *F. pratensis*, *F. panamensis*, and *F. granatensis* but is easily distinguished by the massively broad corymbose inflorescence and by the abrupt base of the involucre with compact outer bracts.

CHIRIQUÍ: Vic. of Las Nubes, 2.7 mi. NW of Río Chiriquí Viejo, W of Cerro Punta, 2,200 m, *Croat 22400* (MO).

4. **Fleischmannia hymenophylla** (Klatt) R. M. King & H. Robinson, Phytologia 19: 203. 1970.

Eupatorium hymenophyllum Klatt, Bull. Soc. Roy. Bot. Belgique 31: 190. 1892 (1893). TYPE: Costa Rica, bords du Río San Pedro entre Général et Buenos Aires, *Pittier 3709* (BR, not seen).

E. valerianum Standley, Publ. Field Mus. Nat. Hist., Bot. Ser. 18: 1474. 1938. TYPE: Costa Rica, colinas de San Pedro de San Ramón, *Brenes 20498* (F).

Fleischmannia valeriana (Standley) R. M. King & H. Robinson, Phytologia 19: 206. 1970.

Erect sparsely branching perennial *herbs* to 2 m tall; stems greenish to reddish, terete, finely striate, with dense reddish puberulence. *Leaves* opposite; blades papyraceous, ovate, to 9 cm long and 4 cm wide, the base rounded to short-cuneate, the margins closely and often sharply serrate, the apex usually narrowly acuminate, the upper surface sparsely puberulous, the lower surface with glandular punctations, puberulous on veins, the veins prominently trinervate from above the base; petioles slender, to 2.8 cm long. *Inflorescence* a lax corymbose panicle with branches bearing heads mostly in small clusters, the ultimate branches 1–6 mm long, densely puberulous. *Heads* ca. 3 mm high with 20–25 florets; involucral bracts 20–25, subimbricate, unequal, in ca. 3 series, bicostate, with narrow scarious margins, the outer surface finely puberulous, the outer bracts short-acute, the inner bracts with broader rounded or slightly mucronate, pale but firm tips; corolla lavender, ca. 2 mm long, with numerous short hairs on outer surface; style branches slender. *Achenes* broadest in upper fourth, distinctly constricted above,

black when mature with black ribs and with numerous bristles above; pappus of ca. 30 scabrous contiguous bristles.

Fleischmannia hymenophylla is known only from Costa Rica and Panama. The species has a distinctively lax corymbose inflorescence with small heads. *Eupatorium valerianum* of Costa Rica seems to be conspecific, having about 20 florets per head rather than about 10 as originally described.

CHIRIQUÍ: Valley of the upper Río Gariche, 1050–1100 m, *Seibert 332* (MO). COCLÉ: Vic. of El Valle, 600–1000 m, *Allen 1206* (F, MO, US). SW of Cerro Pilón, *Croat 22917* (MO). La Mesa, above El Valle, 600–800 m, *Duke 15163* (OS). El Valle de Antón, 1000–2000 ft, *Lewis et al. 2547* (MO).

5. **Fleischmannia microstemon** (Cass.) R. M. King & H. Robinson, Phytologia 19: 204. 1970.—FIG. 22.

Eupatorium microstemon Cass., Dict. Sci. Nat. 25: 432. 1822. TYPE: Jardin du Roi, Paris, origin unknown, *Cassini* (P, not seen).
E. guadalupense Spreng., Syst. Veg. 3: 414. 1826. TYPE: Guadeloupe, *Bertero* (TO?, not seen; P?, not seen).
E. paniculatum Schrad., Ind. Sem. Hort. Götting. 2. 1832, ex Linnaea 8 litt.: 26. 1833, not *E. paniculatum* Miller, 1768.
E. bimatrum Standley & L. O. Williams, Ceiba 3: 64. 1952. TYPE: Honduras, El Zamorano, Morazán, *Standley 13132* (F).
Ageratina bimatra (Standley & L. O. Williams) R. M. King & H. Robinson, Phytologia 19: 212. 1970.

Erect annual *herb* to 1 m tall, sparsely branched; stems yellowish-green to brown, terete, finely striate, glabrescent. *Leaves* mostly opposite, alternate above; blades membranaceous, broadly rhombic-ovate, to 3.7 cm long and 3.0 cm wide, the margins crenulate, the apex short-acute, the upper surface with sparse coarse hairs, the lower surface with glandular punctations, with puberulous veins, the veins prominently trinervate at the base; petioles slender, to 2.5 cm long. *Inflorescence* a lax panicle with loosely cymose branches, the ultimate branches 2–7 mm long, slender, puberulous. *Heads* ca. 4 mm high with 20–35 florets; involucral bracts 15–22, subimbricate, unequal, in ca. 3 series, mostly bicostate, the outer 2 series usually narrowly acute, sparsely short-hirsute, the 2nd series with hairs only along the median line, the inner bracts broad and mostly scarious at the tip, often with a short mucro; corolla lavender or white, ca. 2 mm long, without hairs on lobes; style branches thick. *Achenes* scarcely constricted above, usually with yellow ribs and blackish sides, the ribs and upper lateral surfaces usually scabrid; pappus of 25–30 slender scarcely contiguous bristles. Chromosome number $n = 4$.

Fleischmannia microstemon is a weedy species at lower elevations ranging from Yucatán through Central America into northern South America and the West Indies. Baker (1967) has studied the reproductive biology of the species and suggested derivation from *F. sinclairii*. The differences in leaf texture, inflorescence, involucral bract shape, head size, and the shape and color of the achene all indicate that the two species are not so closely related and that none of the material with a chromosome number of $n = 4$ belongs to *F. sinclairii*.

The species is known by the common name "cucursapi" in Panama, *Duke 14418* (FSU).

B
A
C
D
A.R. Tangerini

BOCAS DEL TORO: Bocas del Toro, *Carleton 92, 70* (both US). Above RR stop at Milla, *Croat & Porter 16293* (MO). Chiriquicito to 5 mi S along Río Guarumo, *Lewis et al. 2003* (MO, REED, UC, US). Water Valley, *von Wedel 723* (MO), *1440, 2742* (both MO, US). CANAL ZONE: Barro Colorado Island, *Standley 31443* (US). DARIÉN: Vic. of Boca de Cupe, ca. 40 m, *Allen 884* (MO, F). Las Delicias, *Carleton 62* (US). Río Pirre, ca. 10 mi S of El Real, *Duke 5446* (MO). Río Pirre near crossing of trail from El Real to Tucutí, *Duke 5196* (MO). PANAMÁ: 7 mi N of Cerro Azul, 2600 ft, *Blum et al. 1826* (FSU). 11 mi S of Goofy Lake, *Correa & Dressler 263* (MO). 3 mi above Goofy Lake near Cerro Azul, *Croat 11579* (MO). Cerro Azul, *Croat 17333* (MO). Ca. 13 mi W of Chepo, *D'Arcy & D'Arcy 6038* (MO). Cerro Azul, 2000 ft, *D'Arcy & D'Arcy 6219B* (MO). Pan-Am. Hwy., near Jenine, Río Cañita, *Duke 3827* (MO). Pan-Am. Hwy. ca. ½ way between El Llano and Río Mamoní, *Duke 5592* (MO). Piria, ca. 150 m, *Duke 14418* (FSU, MO). Cerro Azul, *Dwyer 2650, 2850* (both MO). Cerro Jefe, ca. 1000 m, *Gentry 6752* (MO). S slopes of Cerro Azul, *King 5244* (UC, US). Cerro Jefe, *Kirkbride & Crebbs 7* (MO). 5 mi SW of Cerro Brewster, *Lewis et al. 3511* (MO). Cerro Azul, 2000 ft, *Tyson 2054* (MO); ca. 2100 ft, *6325* (FSU, MO). SAN BLAS: Opposite Achituppu, *Lewis et al. 136* (MO). Around Obaldía, 0–50 m, *Pittier 4369* (US).

6. **Fleischmannia misera** (B. L. Robinson) R. M. King & H. Robinson, Phytologia 19: 204. 1970.

Eupatorium miserum B. L. Robinson, Proc. Amer. Acad. Arts 54: 258. 1918. TYPE: Colombia, falls of the Truando, Chocó, *Schott 2* (F, photo US).

Erect short-lived perennial *herb* to 4 dm tall, laxly and usually sparsely branched; stems yellowish-green to brown, terete, finely striate, densely minutely puberulent. *Leaves* and lower bracts of inflorescence opposite; blades papyraceous, narrowly elliptical, to 4.5 cm long and 1.0 cm wide, the base narrowly cuneate, the margins serrulate beyond widest part, the apex narrowly acute, the upper surface with sparse short coarse hairs, the lower surface sparsely puberulous and glandular punctate, the veins prominently trinervate from the base; petioles slender, to 1.5 cm long. *Inflorescence* a lax panicle with loosely cymose branches, the ultimate branches to 13 mm long, slender, minutely puberulous. *Heads* ca. 4 mm high with ca. 25 florets; involucral bracts ca. 25, subimbricate, unequal, in 2–3 series, mostly bicostate, narrowly acute with narrow scarious margins, the outer bracts with long-attenuate tips; corolla white to lavender, 1.5–2.0 mm long with short hairs on the lobes; style branches usually slender. *Achenes* narrowly oblong with nearly equal constrictions above and below, black when mature with black ribs, scabrid or with short bristles mostly on the ribs; pappus of ca. 25 slender scarcely contiguous to slightly noncontiguous bristles.

The species is known only from the limited area of southern Darién and along the immediately adjacent Pacific coast of Colombia. Relationship is close to *F. sinclairii* from which it differs primarily by the narrower leaves and by a supposedly perennial habit. The similar looking *F. haughtii* R. M. King and H. Robinson of adjacent Colombia differs by the nonglandular-punctate, more membraneous leaves, the glabrous achenes, and the pappus only ½ to ⅔ as long as the corolla.

DARIÉN: Río Sambú, 0–5 mi above Río Venado, *Duke 9263* (MO, OS). Manené to the mouth of the Río Cuasí, *Kirkbride & Bristan 1463* (MO, REED).

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FIGURE 22. *Fleischmannia microstemon* (Cass.) R. M. King & H. Robinson.—A. Habit (× ½).—B. Head (× 5⁹⁄₁₀).—C. Corolla (× 29).—D. Achene (× 25).

7. **Fleischmannia panamensis** R. M. King & H. Robinson, Phytologia 28: 80. 1974. TYPE: Panama, near La Mesa, Coclé, *Croat 13354* (MO).

Erect, branching, coarse perennial *herbs* or *subshrubs* to 2 m tall; stems mostly brownish, terete, finely striate, glabrescent, densely puberulous on the younger parts. *Leaves* opposite; blades papyraceous, broadly rhombic-ovate, to 8 cm long and 6.5 cm wide, the margins shallowly to deeply crenate, the apex broadly acute, rarely slightly acuminate, the upper surface with coarse hairs, the lower surface glandular punctate, the veins prominently trinervate from the base; petioles slender, to 3.5 cm long. *Inflorescence* a corymbose panicle with densely corymbose branches, the ultimate branches 1–4 mm long, puberulous. *Heads* ca. 5 mm high, with ca. 15–20 florets; involucral bracts ca. 18–20, subimbricate, unequal, in 2–3 series, bicostate, short-acute with very narrow scarious margins, glabrous to finely puberulous, the inner bracts with more scarious rounded to mucronate tips; corolla purple to lavender, ca. 3 mm long, without hairs on lobes; style branches rather thick. *Achenes* scarcely constricted above, black with black ribs when mature, sparsely bristled above and on the ribs; pappus of ca. 20–22 scarcely contiguous bristles.

Fleischmannia panamensis is known only from middle elevations in central Panama. The species looks like a coarse *F. microstemon* but is more closely related to the widely distributed *F. pratensis*. *Fleischmannia panamensis* is distinct by its narrower, nearly glabrous, outer involucral bracts with only narrow scarious margins, by the corolla lobes lacking hairs, and by the somewhat thicker style branches.

COCLÉ: Near La Mesa, *Croat 13354* (MO). Cerro Caracoral, ca. 1000 m, *Duke 15085* (OS). La Mesa, above El Valle, 900 m, *Liesner 749* (MO). PANAMÁ: Cerro Campana, *Busey 859* (MO); *Croat 14201* (MO); *Kennedy et al. 2063* (MO); *Lazor 3322* (FSU, MO); Cerro Pilón, 900–1173 m, *Liesner 759* (MO). Cerro Campana, *Porter et al. 4254* (MO).

8. **Fleischmannia pratensis** (Klatt) R. M. King & H. Robinson, Phytologia 19: 205. 1970.

Eupatorium pratense Klatt, Bull. Soc. Roy. Bot. Belgique 31: 193. 1892 (1893). TYPE: Costa Rica, savanes de Boruca, *Pittier 4756* (US, lectotype).
E. roseum Klatt, Bull. Soc. Roy. Bot. Belgique 31: 194. 1892 (1893). TYPE: Costa Rica, clairières du Rodeo de Pacaca, *Pittier 3324* (BR, GH).
E. pacacanum Klatt, Leopoldina, Bot. Beibl. 3. 1895. TYPE: Costa Rica, *Pittier 3324* (BR, GH).

Erect to reclining perennial *herb* or *subshrub* to 1.5 m tall; stems greenish to brown or reddish, terete, finely striate, densely puberulous. *Leaves* mostly opposite, some upper leaves often alternate; blades papyraceous, rhomboidal to narrowly ovate, to 5.5 cm long and 3.5 cm wide, the base truncate to broadly cuneate, the margins usually bluntly serrate-crenate, the apex short-acute to short-acuminate, the upper surface coarsely to finely pilose, the lower surface sparsely to rather densely short-pilose, puberulous on veins, with glandular punctations, the veins prominently trinervate from base; petioles slender, to 3 cm long. *Inflorescence* a broad corymbose panicle with very densely corymbose branches, the heads in glomerate clusters, the ultimate branches 1–3 mm long, puberulous.

Heads 4–5 mm high with 20–25 florets; involucral bracts ca. 20, subimbricate, unequal, in ca. 3 series, bicostate, with broad scarious margins, usually with prominent scattered puberulence on outer surface, the outer bracts with short-acute tips, the inner bracts with broad usually rounded more scarious tips; corolla lavender to white, ca. 2.5 mm long, often with short hairs on the outer surface of the lobes; style branches slender. *Achenes* slightly constricted above, black with black ribs when mature, usually scabrid or with short bristles primarily or exclusively on the ribs; pappus of ca. 25 closely scabrous often basally thickened and usually contiguous bristles.

This species has been called *F. pycnocephala* (Less.) R. M. King & H. Robinson in Panama. The type of true *F. pycnocephala* proves to represent another species that is more common in Mexico, having yellowish ribs on the achenes, more slender noncontiguous pappus setae, corollas without hairs, leaves usually with more obscure glands or no glands, and generally thicker style branches. *Fleischmannia pratensis* has a somewhat overlapping range with *F. pycnocephala* extending from central Mexico southward through Central America into northern South America.

The type of *Eupatorium pycnocephala* Less. from Patlanta, Veracruz, collected by Schiede, is presumed destroyed at Berlin, but a duplicate from the herbarium at Halle (HAL) has been seen. Its most significant feature, the color of the achene, is that of the northern species and the name seems best retained for that entity. However, other characters of the type specimen show some features, such as a few short hairs on the corolla lobes and thicker pappus bristles, that are rare or lacking in other material of the species. The uniquely intermediate nature of the type may indicate hybridization and both species occur in the general area of the type locality.

The type of *Eupatorium pacacanum* from Costa Rica is a variant of *F. pratensis* having minute, scarcely visible stipitate glands instead of prominent glandular punctations on the undersurface of the leaf and having less closely contiguous pappus bristles. Both characters seem to occur independently in a few other specimens of *F. pratensis* and the plants can be regarded as nothing more than a form.

CHIRIQUÍ: Llanos del Volcán, ca. 1300 m, *Allen 1555* (F, MO, US). San Bartolo Limite, 20 km W of Puerto Armuelles, 400–600 m, *Busey 529* (MO). Above Boquete past Princesa Janca coffee finca, *D'Arcy & D'Arcy 6335* (MO). Between El Hato and Lagunas de Volcán, *D'Arcy & D'Arcy 6624* (MO). Bajo Chorro, Boquete, 6000 ft, *Davidson 49* (F, MO, US), *138* (F). Burica Peninsula, 12 mi W of Puerto Armuelles, 400–500 m, *Liesner 194* (MO). 0.5 mi N of El Hato del Volcán, *McDaniel 10074* (FSU). Alto Boquete, *Partch 69-51, 69-78* (both MO). El Boquete, 1000–1300 m, *Pittier 2856* (US). Cerro Vaca, 900–1136 m, *Pittier 5303* (US). Cerro Punta, 1500–2000 m, *Seibert 254* (MO, US). Vic. of Callejón Seco, Volcán de Chiriquí, 1700 m, *Woodson & Schery 498* (MO). Vic. of Bajo Chorro, 1900 m, *Woodson & Schery 639* (MO). Finca Lerida to Boquete, ca. 1300–1700 m, *Woodson et al. 1137* (MO). COCLÉ: Club Campestre, ca. 700 m, *Duke 13267* (MO, US). Cerro Pilón near El Valle, 700–900 m, *Duke 12094* (MO). Ridge S of El Valle, ca. 600 m, *Gentry 6810* (MO). El Valle, *Miller 1829* (US). HERRERA: Vic. of Las Minas, La Peña, *Stern et al. 1770* (MO, US). LOS SANTOS: 17.8 mi S of Macaracas, 1100 ft, *Lewis 1604* (MO). Between Tonosí and Guanico, *Stern et al. 1878* (MO, US). 12 mi S of Macaracas, *Tyson et al. 3071* (MO). PANAMÁ: Alto Llano, 4400 ft, *Maurice 872* (US). Cerro Azul, *Croat 13024* (MO). Cerro Jefe, *D'Arcy 3976* (MO). Finca del Indio, Cerro Jefe, *D'Arcy 5221* (MO). Goofy Lake, *Dwyer 4142* (MO). Cerro Jefe, ca. 1000 m, *Gentry 6765* (MO). Cerro Jefe, 2700 ft, *Tyson 3371* (MO).

9. **Fleischmannia sideritidis** (Benth. in Örsted) R. M. King & H. Robinson, Phytologia 19: 206. 1970.

Eupatorium sideritidis Benth. in Örsted, Vidensk. Meddel. Dansk Naturhist. Foren. Kjøbenhavn 1852: 77. 1852. TYPE: Costa Rica, Ujarras, *Örsted* (C, not seen, photo US).

Erect to decumbent perennial *herbs* to 60 dm tall, rarely branching above base; stems slender, greenish-brown to reddish, terete, finely striate, minutely puberulous. *Leaves* and lower bracts of inflorescence opposite; blades papyraceous, narrowly elliptical to lanceolate, to 7.5 cm long and mostly 1 cm wide, rarely to 1.7 cm wide, the base narrowly cuneate, the margins with 3–6 remote serrations in distal half, the apex narrowly acute, the upper surface sparsely puberulous, the lower surface with glandular punctations, with minute hairs only on veins, the veins prominently trinervate from near base; petioles indistinct, to 1 cm long. *Inflorescence* a lax panicle with lax rather cymose branches, the ultimate branches 2–15 mm long, densely minutely puberulous. *Heads* ca. 5 mm high with ca. 20–25 florets; receptacle rather convex or conical when fresh; involucral bracts ca. 20, subimbricate, unequal, in 2–3 series, mostly bicostate, short- to long-acute with narrow scarious margins, the outer surface glabrous to finely puberulous, the inner bracts with more scarious tips, the apices acute or with a short mucro; corolla lavender, ca. 2.5 mm long, usually with short hairs on lobes; style branches thick. *Achenes* only slightly constricted above, black when mature, often with slightly yellow ribs, scabrous above and on the ribs; pappus of ca. 25 slender bristles with broadened usually contiguous bases.

Fleischmannia sideritidis is known only from Costa Rica and Panama. The Costa Rican plants have generally more pointed involucral bracts than the Panamanian plants. A somewhat similar species found in Guatemala, El Salvador, Honduras, and Nicaragua is *F. imitans* (B. L. Robinson) R. M. King & H. Robinson. It has larger heads containing more florets and more subequal involucral bracts.

CANAL ZONE: Unnamed quebrada entering lake, Río Indio, 70–80 m, *Dodge & Allen 17293* (MO). Banks of Quebrada La Palma and Cañon of Río Chagres, 70–80 m, *Dodge & Allen 17366* (F, MO). Between Peluca Hydrographic Station and Quebrada Peluca, *Steyermark & Allen 17240* (MO). COCLÉ: Vic. of El Valle, 800–1000 m, *Allen 83* (MO, US). La Mesa, above El Valle, 600–800 m, *Duke 15164* (OS). Bismark above Penonomé, *Williams 286* (US). COLÓN: Ca. 2–3 mi up the Río Guanche, 10–20 m, *Kennedy & Foster 2128* (MO). PANAMÁ: Cerro Jefe, *D'Arcy 3979* (MO). Between Cerro Azul and Cerro Jefe, *Dressler 3268* (FSU, MO, US). VERAGUAS: 5 mi NW of Santa Fe, 700–1000 m, *Croat 23174* (MO).

10. **Fleischmannia sinclairii** (Benth. in Örsted) R. M. King & H. Robinson, Phytologia 19: 206. 1970.

Eupatorium sinclairii Benth. in Örsted, Vidensk. Meddel. Dansk Naturhist. Foren. Kjøbenhavn 1852: 79. 1852. TYPE: Costa Rica, Cartago, *Örsted* (C, not seen).

Erect annual *herb* to 1 m tall, sparsely branched; stems yellowish-green to brown, terete, finely striate, minutely puberulous. *Leaves* and many bracts of inflorescence opposite; blades of leaves papyraceous, rhombic, to 5 cm long, basal leaves to 3 cm wide, the margins crenulate above widest part, the apex broadly acute to slightly acuminate, the upper surface with coarse hairs, the lower

surface sparsely puberulous and glandular punctate, the veins prominently trinervate from base; petioles slender, to 2.0 cm long. *Inflorescence* a lax panicle with loosely cymose branches, the ultimate branches to 12 mm long, slender, puberulous. *Heads* ca. 4 mm high with ca. 25 florets; involucral bracts ca. 25, subimbricate, unequal, in 2–3 series, mostly bicostate, narrowly acute with narrow scarious margins, the outer bracts with long attenuate tips; corolla usually lavender, ca. 2 mm long, with short hairs on lobes; style branches usually slender. *Achenes* narrowly oblong with nearly equal constrictions above and below, black when mature, ribs black, scabrid above and on the ribs; pappus of ca. 25 slender scarcely contiguous bristles. Chromosome number $n = 10$.

Fleischmannia sinclairii is a delicately branched species distributed from central Mexico through Central America to Panama. The small heads with the sharply pointed, evenly puberulous involucral bracts distinguish the species from all but the closest relative, *F. misera*. A species of similar appearance, *F. capillipes* (Benth. ex Örsted) R. M. King & H. Robinson, ranging from Mexico to Nicaragua, differs by the subequal, eximbricate involucral bracts and the pappus of usually ten bristles.

CANAL ZONE: Ancón, *Celestine 75* (US). Barro Colorado Island, *Croat 8824, 14941* (both MO). Madden Forest Road 1, *Croat 8934* (MO). Pipeline Road, 2½ mi from gate, *Croat 9367* (F). Guillard Hwy. near Paraíso, *Croat 10140* (MO). Road to LaPita signal station near Summit, *Croat 13957* (MO). Albrook Site, *Dwyer 6580* (MO). Albrook, *Dwyer & Robyns 87* (MO). Chagres, *Fendler 158* (MO, US). Balboa Heights, *Greenman & Greenman 5057* (MO, US). Madden Forest Preserve, Las Cruces Trail, *Lewis et al. 5333* (MO, UC). Empire to Mandinga, *Piper 5501* (US). Culebra, 50–150 m, *Pittier 2147* (US). Valley of Masambi, road to Las Cascadas Plantation, 20–100 m, *Pittier 2670* (F, MO, US). Boy Scout Road, Madden Dam Area, *Porter et al. 4027* (MO, UC). Ancón Hill, *Standley 26318* (US). Summit, *Standley 26943* (US). Old Las Cruces Trail, between Fort Clayton and Corozal, *Standley 29075* (US). Las Cascadas Plantation, near Summit, *Standley 29596* (US). Vic. of Summit, *Standley 30001* (US). Obispo, *Standley 31717* (US). Pueblo Nuevo, *White 300* (MO). Ancón Hill, 600 ft, *Williams 29* (US). CHIRIQUÍ: Ca. 14 mi N of David, 1200 ft, *Lewis et al. 667* (MO, UC, US). COCLÉ: Vic. of Olá, 100–350 m, *Pittier 5056* (US). COLÓN: Río Chagres, region above Gamboa, 25 m, *Allen 4120* (MO). Peluca, ca. 27 km from Transisthmian Hwy. on road to Nombre de Díos, *Kennedy 2636* (MO). DARIÉN: Teotuma, ca. 100 m, *Duke 10065* (MO). Agua Fria, ca. 8 mi N of Santa Fe, 50 m, *Duke 10096* (MO, REED, US). Río Sabana, ca. 4 mi above Santa Fe, 25 m, *Duke 10205* (MO, OS). Near Punta Garachine, *Duke 10476* (MO, OS). Boca Grande Tide Gage, 50 ft, *Duke 15542* (FSU, REED). Hydro Camp Pico Pendejo on Río Sabana, 50 ft, *Duke 15444* (MO, OS). Mouth of Lara River, *Tyson & Loftin 3857* (FSU, MO). HERRERA: 4 mi S of Los Pozos, *Tyson 2656* (FSU, MO). LOS SANTOS: Loma Prieta, 800–900 m, *Duke 11878* (MO, OS). PANAMÁ: Río Las Lajas, ca. 20 m, *Allen 1610* (F, MO, US). Sabanas, N of Panama City, *Paul 601* (US). Road to Cerro Campana, *Correa & Dressler 845* (FSU, MO, US). Between Capira and Potrero, 80–130 m, *Dodge & Hunter 8621* (MO). Isla del Rey, *Duke 9549* (MO, OS, US). 10–15 km from Bayano crossing on trail to Santa Fe, *Gentry 3826* (MO). Sabanas near Chepo, 30 m, *Hunter & Allen 29* (F, MO). Río Tocumen, N of Chepo Road, *Hunter & Allen 215* (F, MO). Cerro Campana, road to Sulin, ca. 650 m, *Kennedy et al. 2037* (MO). Cerro Campana, *Lazor 2215* (FSU, MO). Chimán, *Lewis et al. 3319* (MO). Río Tapia, *Standley 28121* (US). Near Matías Hernández, *Standley 28928* (US). VERAGUAS: La Mesa, *Tyson 6066* (FSU).

11. **Fleischmannia tysonii** R. M. King & H. Robinson, Phytologia 28: 82. 1974. TYPE: Panama, W slope of El Barú, Chiriquí, *Tyson & Loftin 6116* (US).

Erect perennial *shrub* to 2 m tall; stems greenish to brown, terete, finely striate, densely hirtellous with brownish to reddish hairs. *Leaves* opposite; blades

papyraceous, broadly ovate, to 9 cm long and 7 cm wide, the base broadly rounded or cordate, the margins bluntly serrate-crenate to doubly serrate-crenate, the apex acute to scarcely acuminate, the upper surface pilose, the lower surface densely pilose, tomentose on veins, without glandular punctations, the veins prominently trinervate from at or near base; petioles slender, to 2.5 cm long. *Inflorescence* a broad corymbose panicle with compact corymbose branches, the ultimate branches 2–4 mm long, hirtellous. *Heads* 5–6 mm high with 20–25 florets; involucral bracts ca. 20, subimbricate, unequal, in 3–4 series, bicostate, mostly short-acute to minutely mucronate with broad often prominent scarious margins, the outer surface pilose to puberulous, the inner bracts with more rounded more scarious minutely fimbriate tips; corolla lavender to purple, ca. 3 mm long, with few to many short hairs on outer surface of lobes; style branches slightly thickened distally. *Achenes* slightly constricted above, black with black ribs when mature, with many bristles almost exclusively on the ribs; pappus of 22–25 scabrous slender noncontiguous bristles.

Fleischmannia tysonii is apparently endemic to the Volcán Chiriquí. Closest relationship is to *F. chiriquensis* from the nearby Cerro Punta area. The present species is distinct by the shrubby rather subscandent habit, by the densely pubescent leaves, by the noncontiguous pappus bristles, and by the many short bristles on the ribs of the achene.

CHIRIQUÍ: 8 mi NE of El Volcán, 8100–8400 ft, *Tyson 843* (FSU, MO). W slope of El Barú, 7000–8000 ft, *Tyson & Loftin 5982* (FSU). W slope of El Barú, 8000–9000 ft, *Tyson & Loftin 6116* (US, FSU), *6117* (FSU, MO).

22. GONGROSTYLUS

Gongrostylus R. M. King & H. Robinson, Phytologia 24: 387. 1972. TYPE: *Eupatorium costaricense* Kuntze.

Sparingly branched slender *vines* with terete subglabrous stems. *Leaves* opposite with short distinct petioles; blades ovate, the base rounded, the margins serrate, the veins trinervate from near base. *Inflorescence* terminal and axillary, corymbose-paniculate, the ultimate branches often long and slender. *Heads* discoid with ca. 20 florets; involucral bracts subimbricate, in 3–4 very unequal series, narrowly lanceolate to linear; receptacle slightly convex, glabrous; corolla narrowly funnelform, the lobes triangular with glands on outer surface; anther collars elongate with short-oblong to elongate cells, the cell walls with transverse annular thickenings, the anther appendage short, only half as long as wide; style base with nodulose enlargement, densely hirsute, the style appendages narrow and slightly mamillose below, greatly enlarged and smooth apically. *Achenes* prismatic with 5 ribs, glabrous; carpopodium large, forming a distinct short cylinder, the basal row of cells greatly enlarged, numerous upper rows of cells small and subquadrate, the cell walls thickened; pappus of ca. 30 scabrous bristles in 1 series, persistent, the bristles scarcely narrowed toward tips, the apical cells subacute. *Pollen* with short spines.

Gongrostylus is a monotypic tropical American genus readily distinguished among the Eupatorieae of Panama by the greatly enlarged tips of the style

branches. In spite of the difference in appearance, the genus is closely related to *Ayapana*, having the same distinctive carpopodium structure and the same type of enlargement of the style base.

Literature:

King, R. M. & H. Robinson. 1972. Studies in the Eupatorieae (Asteraceae). CIV. A new genus, *Gongrostylus*. Phytologia 24: 387–388.

1. **Gongrostylus costaricensis** (Kuntze) R. M. King & H. Robinson, Phytologia 24: 388. 1972.—FIG. 23.

Eupatorium costaricense Kuntze, Rev. Gen. Pl. 1: 337. 1891. TYPE: Costa Rica, Angostura, 1600 m, *Kuntze* (K).

Somewhat woody, scandent, slender *epiphyte* with few branches; stems terete, striate, sparsely to coarsely hirsute. *Leaves* opposite; blades ovate, to 9.5 cm long and 4 cm wide, the base rounded with a slight acumination, trinervate, the margins with few sharp small teeth, the apex short- to rather long-acuminate, the surface sparsely short-hirsute; petioles short, distinct, 3–8 mm long. *Inflorescence* terminal and axillary, laxly corymbose, the ultimate branches 5–20 mm long, slender, puberulous. *Heads* 8–10 mm high with ca. 20 florets; involucral bracts ca. 25, subimbricate, in ca. 3 series, 2.5–10.0 mm long, ovate-lanceolate to linear-lanceolate, sharply acute, glabrous to slightly puberulous on outer surface, weakly bicostate; corolla 6.0–6.5 mm long, glabrous with glands on outer surface of lobes, the lobes very small, slightly longer than wide; enlarged style tips ca. 0.8 mm long and 0.3 mm wide. *Achenes* ca. 2 mm long, prismatic, glabrous; pappus mostly 4–6 mm long with ca. 30–35 bristles. *Pollen* ca. 20 μ in diameter.

Gongrostylus costaricensis has been known from two widely separated localities in Costa Rica and Ecuador. The new collections from Panama indicate a more continuous distribution.

SAN BLAS: Road from El Llano to Cartí-Tupile, continental divide to 1 mi from Divide, 300–500 m, *Liesner 1296* (MO). VERAGUAS: 5–8 km beyond Escuela Agricola Alto Piedra, 730–770 m, *Croat 25925* (MO). Río Dos Bocas, 11 km beyond Agricultural School, 450–550 m, *Croat 27537* (MO, US).

23. HEBECLINIUM

Hebeclinium DC., Prodr. 5: 136. 1836. TYPE: *Eupatorium macrophyllum* L.

Erect large *herbs* or *subshrubs*, sparingly branched. *Leaves* always opposite; blades broadly ovate to deltoid, usually serrate; petioles rather long. *Inflorescence* a corymbose panicle or lax cyme. *Heads* discoid with 20–80 florets; involucre of 25–40 bracts, in 3–5 series, the outer bracts persistent; receptacle hemispherical, often with center broken off, glabrous to densely hirsute, sclerified throughout (parenchymatous internally in one species); corolla narrowly tubular, 5-lobed, the outer surface of corolla glabrous below, the lobes usually longer than wide, usually with prominent multicellular uniseriate hairs and a few glands, the inner surface of some species with numerous hairs, the corolla cells narrow with sinuous walls; anther collar often slender, with many quadrate cells in lower part, the cell

FIGURE 23. *Gongrostylus costaricensis* (Kuntze) R. M. King & H. Robinson.—A. Habit (× ½).—B. Head (× 2⅘).—C. Corolla (× 6⁹⁄₁₀).—D. Style (× 6⁹⁄₁₀).—E. Achene (× 6⁹⁄₁₀).

walls rather thin with indistinct annular thickenings, the anther appendage ovate, longer than wide; style base not enlarged, glabrous, the style appendages narrow throughout, slightly mamillose. *Achenes* prismatic, often slightly curved, 4–5-ribbed, bristles sometimes present; carpopodium scarcely distinct, only a few

rows of short cells at lower margin, the area of longer upper cells merging with sides of achene and extending up ribs; pappus of ca. 30–40 scabrous bristles, the apical cells acute.

Hebeclinium contains about 18 species found mainly in northern South America. Three species have been collected in Panama. Members of the genus are distinguished primarily by the receptacle but the very slender style appendage is also a notable feature.

Hebeclinium has usually been recognized at the sectional level for members of "*Eupatorium*" having hairs on the receptacle. The concept contained many but not all members of the related generic series, *Hebeclinium*, *Bartlettina* and *Decachaeta*, where there seems to be a tendency toward pubescent receptacles. Section *Hebeclinium* suffered most by the inclusion of extraneous elements such as *Polyanthina* which is related to *Ayapana*, and *Urolepis* which is related to *Gyptis*.

Literature:

King, R. M. & H. Robinson. 1969. Studies in the Compositae-Eupatorieae, IX. A review of the genus *Eupatorium* section *Hebeclinium* in Colombia. Sida 3: 321–326.

——— & ———. 1971. Studies in the Eupatorieae (Asteraceae) XXXVII. The genus *Hebeclinium*. Phytologia 21: 298–301.

a. Heads with 50–80 florets; inflorescence a corymbose-panicle; base of leaf blade usually truncate to cordate ..... 2. *H. macrophyllum*
aa. Heads with 20–40 florets; inflorescence a lax cyme; base of leaf blade cuneate.
b. Heads with 20–25 florets; leaf margins doubly serrate ..... 3. *H. reedii*
bb. Heads with ca. 40 florets; leaf margins crenulate ..... 1. *H. costaricense*

1. **Hebeclinium costaricense** R. M. King & H. Robinson, Phytologia 23: 407. 1972. TYPE: Costa Rica, near La Laguna, 6 to 8 km S of Villa Quesada, 1200 m, Alajuela, *Molina et al. 17545* (F).

Shrubs or small *trees* to 7 m tall; stems terete, faintly striate, puberulous to hirtellous. *Leaves* opposite; blades papyraceous, broadly ovate, mostly 9–16 cm long and 6–9 cm wide, the base broadly cuneate, the margins slightly crenulate, the apex slightly acuminate, the veins hirtellous, the venation pinnate, the secondary veins ca. 5 pairs, ascending at ca. 45° angle; petioles mostly 3–4 cm long. *Inflorescence* a loose cyme, the ultimate branches 1–20 mm long, hirtellous. *Heads* mostly in clusters of 3, ca. 6 mm high with ca. 40 florets; involucral bracts ca. 40, imbricate, strongly unequal, in 4 series, narrowly oblong, the apices obtuse, the outer surface with ca. 3 striae, puberulous above; receptacle hemispherical, nonparenchymatous, pilose; corolla white, ca. 3.4 mm long, narrowly tubular, slightly funnelform above, glabrous below and within, the lobes oblong-ovate, ca. 0.4 mm long and 0.3 mm wide with cluster of hairs on outer surface. *Achenes* ca. 1.5 mm long, sparsely glanduliferous; pappus of ca. 27 bristles, ca. 2.5 mm long, the apex distinctly dilated, the apical cells acute to subacute.

The species is known only from Costa Rica and Panama.

COCLÉ: El Valle, behind Club Campestre, *Croat 14270* (MO). N slope and summit of Cerro Pilón, 900–1173 m, *Croat 22935* (MO). El Valle, Cerro Pilón, 3000 ft, *Duke 14984* (MO). Cerro Caracoral, *Kirkbride 1116* (MO). PANAMÁ: Near Summit of Cerro Campana, 1000 m, *Croat 22831* (MO).

2. **Hebeclinium macrophyllum** (L.) DC., Prodr. 5: 136. 1836.—FIG. 24.

Eupatorium macrophyllum L., Sp. Pl., ed. 2. 1175. 1763. TYPE: America, Plumier sp. 10, *pl. 129.*

Ageratum guianense Aubl., Hist. Pl. Guiane 2: 800. 1775. TYPE: French Guiana, *Aublet* (BM?, not seen).

Eupatorium molle Swartz, Prodr. Veg. Ind. Occ. 111. 1788, nom. illeg., incl. sp. prior. TYPE: Jamaica, *Swartz* (S?, not seen).

Coleosanthus tiliaefolius Cass., Dict. Sci. Nat. 24: 519. 1822. SYNTYPES: Saint-Domingue, Herb. Desfontaines. Cayenne, Herb. Desfontaines (P?, FI?, not seen).

Eupatorium populifolium Mart., Flora 20, Beibl. 2: 105. 1837, not *E. populifolium* H.B.K., 1818. TYPE: Brasil, Rio de Janiero, *Martius 139* (M?, not seen).

E. dryadeum DC., Prodr. 7: 269. 1838, new name for *E. populifolium* Mart. TYPE: Brasil, *Martius 139* (M?, not seen).

Ageratum coeruleum Sieber ex Baker in Mart., Fl. Bras. 6(2): 345. 1876, nom. nud. TYPE: Martinique, *F. Kohaut 192* (B, destroyed).

Erect *herbs* or small *shrubs to* 2.5 m tall; stems terete, faintly striate, densely tomentellous. *Leaves* opposite; blades thinly papyraceous, broadly ovate, to 15 cm long and 20 cm wide, the base usually truncate or cordate, the margins crenulate-dentate, the apex acuminate, the upper surface dark green, sparsely puberulous to nearly glabrous, the lower surface light green, densely tomentellous, the venation trinervate from base; petioles to 10 cm long. *Inflorescence* a loose many-headed corymbose panicle, the ultimate branches to 1 cm long, densely puberulous. *Heads* ca. 4.5 mm high with ca. 50–80 florets; involucral bracts green, ca. 30, imbricate, unequal, in 4–5 series, ovate to oblong-lanceolate, the outer surface with ca. 4–5 striae, densely puberulous, the inner bracts with more narrowly acute tips; receptacle hemispherical, without parenchyma, densely hirsute; corolla white or pink, narrowly tubular, ca. 3.5 mm long, the lobes ca. 0.2 mm long, about twice as long as wide with numerous hairs on outer surface. *Achenes* ca. 1.5 mm long, mostly glabrous with some glands above; pappus of ca. 30–35 slender somewhat scabrous bristles, the apical cells acute.

Hebeclinium macrophyllum is a common and widely distributed plant in the American tropics ranging from Mexico south to Argentina and east through the West Indies. The more narrowly acute, grayish-green involucral bracts give a distinctive appearance to the heads. In the Province of Panama the species has the common name "roble," *Duke 5819* (MO).

BOCAS DEL TORO: Almirante, *Blum 1342* (MO). Bocas del Toro, *Carleton 228* (US). Almirante, *Cooper 172* (F). Changuinola Valley, *Dunlap 286* (US). Changuinola near Chiriquí Land Company, *Dwyer 5112* (US). Shepherd Island, *McDaniel 5163* (FSU, MO). Swan Key, 2 km N of Isla Colón, *Tyson & Loftin 6295* (FSU, MO, US). Water Valley, *von Wedel 615* (MO). Water Valley, vic. of Chiriquí Lagoon, *von Wedel 1544, 1576, 1680, 1774*

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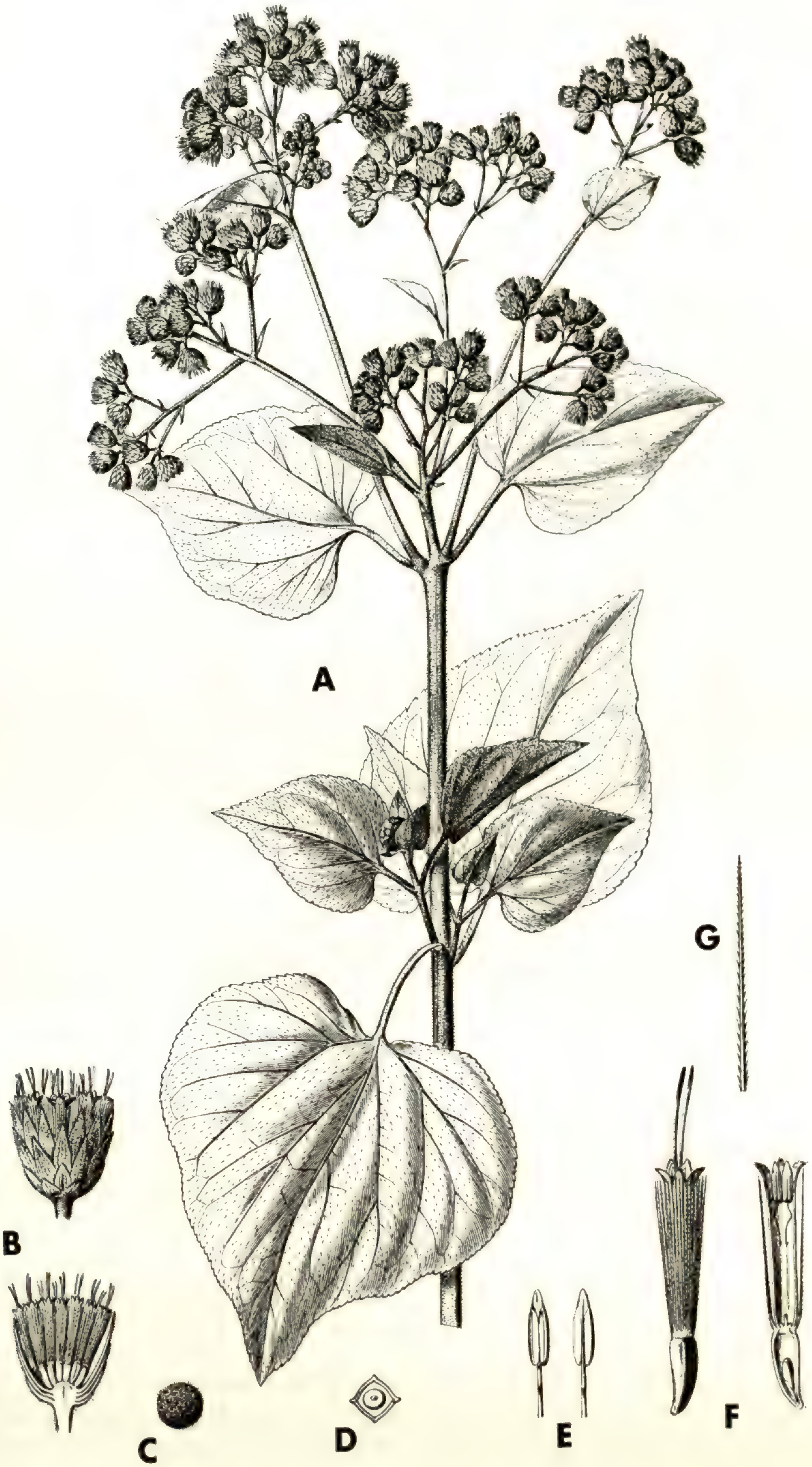
FIGURE 24. *Hebeclinium macrophyllum* (L.) DC.—A. Habit (× ½).—B. Heads (× 1 9/10).—C. Receptacle (× 3 4/5).—D. Achene cross section (× 5 3/5).—E. Stamens (× 11 3/10).—F. Florets (× 5 3/5).—G. Pappus bristle (× 11 3/10). [After Martius, Flora Brasiliensis 6(2): plate 92. 1876.]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(all MO, US). Vic. of Nievecita, 0–50 m, *Woodson et al. 1820* (MO). CANAL ZONE: Barro Colorado Island, *Aviles* 5 (MO). Hills N of Frijoles, *Standley 27626* (US). Vic. of Salamanca Hydrographic Station, Río Pequení, 80 m, *Woodson et al. 1566* (MO, US). CHIRIQUÍ: Puerto Armuelles, *Davidson 1080* (F). 20 km W of Puerto Armuelles, 400–600 m, *Busey* 535 (MO). Vic. of San Félix, 0–120 m, *Pittier 5188* (US). DARIÉN: Río Pirre, 20 mi W of El Real, *Duke 5191* (MO). Ca. 2 mi NW of Yaviza, *Duke 6530* (MO). Quebrada Nigua, below Santa Fe, *Duke* 8828 (MO, OS). Tiotuma, ca. 100 m, *Duke 10069* (MO). Agua Fria, 8 mi N of Santa Fé, 50 m, *Duke 10118* (FSU, OS). Camp Tiotuma, 164 ft, *Duke 15510* (OS, REED). 3 mi E of Santa Fe, *Tyson et al. 4675* (MO). Boca de Cupe, *Williams 717* (US). LOS SANTOS: Loma Prieta, 800–900 m, *Duke 11836* (MO, OS), *11846* (MO). Vic. of headwaters of Río Pedregal, 25 mi SW of Tonosí, 2500–3000 ft, *Lewis et al. 2914* (MO). PANAMÁ: Cerro Azul, *Croat 17329* (MO). Dam site, ca. 4 mi S of Cañita, *D'Arcy & D'Arcy 6053* (MO). Road to Cerro Azul, 2000 ft, *D'Arcy & D'Arcy 6218* (MO). Pan-Am. Hwy. near Jenine, Río Cañita, *Duke* 3858 (MO). Vic. of El Llano, *Duke* 5819 (MO). Cerro Jefe, 10–13 mi S of Goofy Lake, *Duke 8007* (MO, OS). Cerro Jefe, *Duke* 9359 (MO, OS). Goofy Lake to 1.5 mi S of Goofy Lake, ca. 1800 ft, *Dwyer & Hayden* 8035 (MO, REED, US). Cerro Jefe, ca. 1000 m, *Gentry 6747* (MO). Tributary of Río Chagres, 5 mi SW of Cerro Brewster, ca. 1000 ft, *Lewis et al. 3524* (MO). Río Tapia, *Standley* 28283 (US). E slope of Cerro Jefe, 2700 ft, *Tyson 3369, 3421* (both MO). Cerro Jefe, *Tyson et al. 4297* (FSU, MO). Cerro Azul, near Finca Urano, ca. 2500 ft, *Tyson 6509* (FSU).

3. **Hebeclinium reedii** R. M. King & H. Robinson, Phytologia 23: 406. 1972. TYPE: Panama, Cerro Pirre, Darién, *Bristan 464* (US, holotype; MO, isotype).

Erect *subshrubs* to 1–2 m tall?; stems terete, densely hirsute. *Leaves* opposite; blades papyraceous, broadly ovate, to 12 cm long and 8 cm wide, the base broadly cuneate, the margins doubly serrate, the apex distinctly short-acuminate, the upper surface with veins short-hirsute, the lower surface with veins and veinlets hirsute, the venation pinnate, the secondary veins with ca. 5 pairs, ascending at 45° angles; petioles 3–4 cm long. *Inflorescence* a loose cyme, the ultimate branches 1–20 mm long, short-hirsute. *Heads* mostly in clusters of 3, ca. 6 mm high, with 20–25 florets; involucral bracts ca. 40, imbricated, strongly unequal, in 4 series, narrowly oblong, the apices obtuse, the outer surface with ca. 3 striae, puberulous above; receptacle strongly convex, without parenchyma, pilose; corolla white, ca. 3 mm long, tubular below, narrowly funnelform above, glabrous below and within, the lobes triangular, ca. 0.4 mm long and wide with cluster of hairs on outer surface. *Achenes* ca. 2 mm long, glabrous; pappus with ca. 25 bristles, ca. 2.5 mm long, the apex distinctly dilated, the apical cells subacute.

Hebeclinium reedii is known only from the type locality in eastern Panama. The heads have fewer florets and less hemispherical receptacles than in most species of *Hebeclinium*.

DARIÉN: Cerro Pirre, *Bristan 464* (MO, US).

24. HETEROCONDYLUS

Heterocondylus R. M. King & H. Robinson, Phytologia 24: 389. 1972. TYPE: *Eupatorium vitalbae* DC.

Erect or climbing *herbs*, *subshrubs* or *shrubs*, sparingly branched. Lower *leaves* opposite, the upper leaves often alternate; the blades ovate to narrowly oblong, entire to serrate; petioles short. *Inflorescence* few to many branched,

paniculate to cymose. *Heads* discoid with 20–80 florets; involucral bracts 15–30, imbricate to subimbricate, strongly unequal to subequal, in 3–5 series, spreading when mature; receptacle flat to slightly convex, glabrous; corolla narrowly funnelform, 5-lobed, the lobes triangular, usually distinctly longer than wide, smooth, glabrous or with a few glands, the corolla cells with mostly sinuous walls; anther collars often thickened above, the lower cells subquadrate or wider, the upper cells oblong to narrowly oblong, the cell walls with annulate thickenings, the anther appendage longer than wide; style base distinctly enlarged, glabrous or hirsute, the style branch broadly linear, smooth to short-papillose. *Achenes* with 5 ribs, the ribs with short bristles or glands, the lower part of achene long-tapered; carpopodium distinct, somewhat asymmetrical with sinuous trace, stopper-shaped, the cells subquadrate, in many series, with distinctly thickened walls; pappus bristles 20–30 in one series, scabrous, the apices unenlarged to gradually dilated, the apical cells acute.

Heterocondylus is a genus of about 12 species found mainly in Brazil. Only one species reaches northern South America and Central America.

Literature:

King, R. M. & H. Robinson. 1972. Studies in the Eupatorieae (Asteraceae). CV. A new genus, *Heterocondylus*. Phytologia 24: 389–392.

1. **Heterocondylus vitalbae** (DC.) R. M. King & H. Robinson, Phytologia 24: 391. 1972.—Fig. 25.

Eupatorium vitalbae DC., Prodr. 5: 163. 1836. TYPE: Brasil, near Rio de Janiero, *Lund* 1834 (G-DC, not seen, US, microfiche).
Campuloclinium surinamense Miq., Linnaea 17: 69. 1843. TYPE: Surinam, prope flumen Commewyne, *Focke 662* (U, photo US).
Eupatorium ecuadorae Klatt, Ann. K. K. Naturhist. Hofmus. 9: 356. 1894. TYPE: Ecuador, *Jameson* (GH, sketch and fragment, not seen).

Scandent woody *herbs* or *shrubs* to 6 m tall with few branches; stems finely striate, terete, sparsely puberulous. *Leaves* and branches of inflorescence opposite; blades coriaceous, elliptic-ovate to ovate-lanceolate, to 12 cm long and 7 cm wide, the base rounded to slightly cuneate, the margins serrate, the apex sharply acute to slightly acuminate, glabrate with slight pubescence on veins, the veins prominently trinervate from base; petioles to 1.5 cm long. *Inflorescence* a loose panicle to 15 cm wide and 25 cm high, the ultimate branches mostly 1–2 cm long, densely puberulous. *Heads* ca. 1.2 cm high with 60–65 florets; involucral bracts ca. 20, subimbricate, subequal, the outer bracts ovate to oblong, apically acute, 5–8 mm long, the outer surface 4–8 costate, puberulous, the inner bracts mostly lanceolate, to 1 cm long, slightly deciduous, the apex narrowly acute, sometimes pink, the outer surface mostly glabrous; receptacle slightly convex; corolla white to pink or purple, ca. 8 mm long, narrowly funnelform, the tube narrow below, the lobes ca. 0.5 mm long, glabrous; style base glabrous. *Achenes* ca. 3.5 mm long, fusiform, 4–5 ribbed, ribs with short bristles; carpopodium short and broad with distinct upper rim, stipitate; pappus of ca. 20 scabrous deciduous bristles, ca. 7 mm long, the tips slightly enlarged.

FIGURE 25. *Heterocondylus vitalbae* (DC.) R. M. King & H. Robinson.—A. Habit (× 2/5).—B. Head (× 2 4/5).—C. Achene (× 6 9/10).—D. Corolla (× 6 9/10).—E. Style (× 6 9/10).

Heterocondylus vitalbae is widely distributed from Honduras south to Peru and Brazil. The moderately coarse plants with often slightly nodding heads present a distinctive appearance.

CANAL ZONE: Barro Colorado Island, *Croat* 7222, 7796, 8666, 8776 (all MO). 1 mi N of Summit Gardens, *Croat* 9095 (MO). Reservoir W of Cocoli, *Croat* 9166 (MO). Pipeline Road, *Croat* 9329, 9363 (both F). CHIRIQUÍ: 2–8 km N of Cañas Gordas (Costa Rica), 1000–1100 m,

Busey 658 (MO). 6 km S of Puerto Armuelles, *Busey* 692 (MO). Palo Santo, 3 mi N of Volcán, *Croat* 13543 (MO). Burica Peninsula, above Quebrada Yerbazales, 200 m, *Croat* 22588 (MO). Bajo Mono, Boquete, 4000 ft, *Davidson* 537 (F, MO). 14 mi N of David, 1200 ft, *Lewis et al.* 669 (MO, US). Burica Peninsula, 12 mi W of Puerto Armuelles, 400–500 m, *Liesner* 196 (MO). El Boquete, 1000–1300 m, *Pittier* 2901 (US). COCLÉ: Bismark above Penonomé, *Williams* 574 (US). DARIÉN: Caña and vic., 2000–6500 ft, *Williams* 748 (US). HERRERA: 10 mi S of Ocú, *Tyson et al.* 2870 (FSU, MO). LOS SANTOS: Loma Prieta, 800–900 m, *Duke* 11902 (MO). Loma Prieta, Cerro Grande, 2400–2800 ft, *Lewis et al.* 2236 (MO). Between Sabanas and Río Yguana, *Macbride* 2639 (F, US). Vic. of Bella Vista, *Piper* 5348 (US). 16 mi S of Macaracas at Quebrada Bejuco, *Tyson et al.* 2926 (MO). PANAMÁ: Cerro Jefe, 2700 ft, *Blum & Duke* 2179 (MO). Road to Cerro Campana, *Correa & Dressler* 844, 847 (both MO). Cerro Jefe, 10–13 mi S of Goofy Lake, *Duke* 8008 (MO, OS). Cerro Jefe, *Duke* 9419 (MO, US). Cerro Campana, 3000 ft, *Duke* 10748 (MO, REED). Cerro Campana, 850 m, *Liesner* 628 (MO). Taboga Island, *Miller* 1860 (US). Cerro Campana, *Porter et al.* 4199, 4308 (both MO). Río Tapía, *Standley* 30655 (US). Cerro Jefe, 2700 ft, *Tyson* 3361 (MO). Cerro Azul, *Tyson* 5379 (MO). Cerro Jefe, *Wilbur & Weaver* 11344 (F, MO). VERAGUAS: Headwaters of Río Cañazas, 300–600 m, *Allen* 177 (MO, US). 2 mi W of Santa Fe, 400–800 m, *Liesner* 843 (MO).

25. ISOCARPHA

Isocarpha R. Brown, Trans. Linn. Soc. London 12: 110. 1817. TYPE: *Calea oppositifolia* L.

Erect perennial *herbs*, branching mostly from base, the bases sometimes creeping. *Leaves* opposite or alternate, sessile or with narrowly winged petioles, with or without basal auricles; blades slightly to strongly trinervate near base, the margins entire to slightly toothed, usually with numerous glandular punctations on surface. *Inflorescence* a lax panicle, sometimes leafy, the branches with heads single or in small clusters. *Heads* discoid, often becoming elongate and amentiform usually with more than 100 florets; involucral bracts eximbricate, in 1–2 series, lanceolate; receptacle highly conical, florets subtended by paleas resembling involucral bracts; corolla narrowly funnelform with a distinct tube, the glands on outer surface mostly on tube and lobes, the lobes 5, triangular, longer than wide, not papillose or with some papillae on inner surface near margin, the corolla cells elongate with sinuous walls; anther collar slender, the cells mostly short-oblong with walls prominently annulate, the exothecial cells subquadrate, the anther appendage longer than wide; style base with distinct enlargement, the style branches without glands, the appendages rather short and tapering, often strongly curled, laxly long-papillose. *Achenes* prismatic with 5 ribs, base narrowed with or without bristles; carpopodium short, asymmetric, with small quadrate cells in few to many rows, the basal row not enlarged; pappus lacking. *Pollen* 18–20 μ in diameter, with short spines.

Isocarpha is a genus of about 12 species ranging from the southwestern United States through Mexico and Central America to the West Indies and South America. Only one species has been collected in Panama.

The genus *Isocarpha* has traditionally been placed in the tribe Heliantheae and the members of the genus show a number of the characters commonly used to distinguish that tribe, including, shorter and more laxly papillose style appendages, densely paleaceous receptacles, and a reduced pappus. Nevertheless, the genus is without close relatives in the Heliantheae and close relatives are

evident in the Eupatorieae. In the latter tribe the genus *Ayapana* has the same form of style appendage and one species of *Ayapana* has a reduced pappus. *Ayapana* is, in turn, related by carpopodium structure and the usually capillary pappus to other members of the Eupatorieae with larger style appendages. The proper relationship of *Isocarpha* is confirmed by the structure of the anther and the style base. The annulated cells of the collar, the exothecial cells with thickenings on all walls, the flat appendage composed of only two cell layers, the pollen 18–20 μ in diameter, and the papillose to hirsute style base of one species are all characters common in the Eupatorieae but unknown in the Heliantheae.

1. **Isocarpha oppositifolia** (L.) R. Brown, Trans. Linn. Soc. London 12: 110. 1817.—FIG. 26.

Calea oppositifolia L., Sp. Pl., ed. 2. 1179. 1763. TYPE: Jamaica, *P. Browne* (Herb. Linnaeus 984.2, not seen, US, microfiche).

Erect perennial *herbs* to 1 m tall; stems, leaves and branches of inflorescence bearing slender nonglandular puberulence and few to many glandular punctations; stems greenish to pale brown, terete to slightly hexagonal, scarcely striate, minutely puberulous. *Leaves* and all but upper bracts of inflorescence opposite; blades narrowly elliptical to lanceolate, to 9 cm long and 2.5 cm wide, the base narrowly cuneate and decurrent on petiole, the margins entire to slightly serrulate, the apex narrowly acute, the surface with dense puberulence, the hairs stiff and slender, the veins prominently trinervate from near base; petioles indistinct to ca. 5 mm long, usually slightly winged. *Inflorescence* with long branches bearing heads singly or in clusters of 2–6, usually in clusters of 3. *Heads* 8–10 mm high or higher when older, usually with more than 100 florets; involucral bracts ca. 15, subequal, lanceolate, ca. 4 mm long, puberulous and glandular-punctate on outer surface, bicostate with costae fused above into stout projecting tip; paleas very similar to involucral bracts but with wider scarious margins and more rounded or truncate tip, the fused costae abruptly projecting as mucro; corolla white, ca. 2 mm long, glands few, sometimes a few stiff short hairs on lobes, the lobes with papillae on inner surface near tip and on margins; anther appendages triangular to oblong, ca. 250 μ long and 150 μ wide. *Achenes* ca. 1.5 mm long, glabrous; carpopodium small but distinct with up to 25 layers of small cells on wider part; pappus lacking.

The species is widespread from the southwestern United States through Mexico and Central America to the West Indies and northern South America.

COCLÉ: Aguadulce, near sea level, *Pittier 4830* (US). HERRERA: Vic. of Chitré, ca. 20 m, *Allen 1088* (MO, US). 4 mi. S of Los Pozos, *Tyson 2641* (MO). LOS SANTOS: Monagre Beach, 5 mi. SE of Chitré, *Tyson et al. 3054* (MO).

26. KOANOPHYLLON

Koanophyllon Arruda da Camara, Discurso sobre utilidade da instituicâo de jardins nas principaes provincias do Brazil, . . . p. 38? 1810.

Shrubs or small *trees* with few to many branches, the branches sometimes long and arching. *Leaves* opposite with short distinct petioles; blades broadly

FIGURE 26. *Isocarpha oppositifolia* (L.) R. Brown.—A–B. Habit ($\times$ 4/5).—C. Head ($\times$ 2^9/$_{10}$).—D. Corolla ($\times$ 14^7/$_{10}$).—E. Achene and style ($\times$ 14^7/$_{10}$).

lanceolate to elliptical (pinnately lobed in one species), the base acute to truncate or cordate, the lower surface with few to many glands, without lacticifers in areoles. *Inflorescence* a lax corymbose or pyramidal panicle, the branches corymbose to spicate. *Heads* discoid with 6 to ca. 20 florets; involucral bracts 7–16, eximbricate to subimbricate, unequal to subequal, spreading at maturity, the innermost bracts sometimes deciduous; receptacle glabrous, flat to slightly convex; corolla tubular, the lobes short-triangular with inner and outer surfaces smooth, numerous capitate glands on outer surface, the cells of the corolla mostly narrow with sinuous walls; anther collar elongate, usually with numerous quadrate cells below, the cell walls usually inornate (one species with annular thickenings), the exothecial cells subquadrate to wider than long, the anther appendage usually wider than long, sometimes very short, the apical margin slightly to strongly recurved, the inner surface often with a median longitudinal groove; style base not enlarged, glabrous, the style appendage distinctly enlarged apically, smooth at tip, without glands. *Achenes* prismatic with 5 ribs and with bristles, glands few or none; carpopodium short and distinct, usually narrowed below, the cells small and subquadrate in many series, the cell walls slightly thickened; pappus with long or short bristles or lacking, the bristles 15–40, scabrous, persistent, the apical cells acute. *Pollen* of Panamanian species all with extremely short spines.

The genus *Koanophyllon* contains 107 species and ranges from Paraguay and Brazil northward along the Andes, reaching the West Indies, Central America, Mexico, and the southwestern United States, with one species in Florida. Two species are sources of bluish or greenish dyes.

Grashoff & Beaman (1970) have noted the elongate many-headed inflorescences, the reduced anther appendages, the less spinose pollen, and the probability of wind pollination in various species of the Eupatorieae that are now placed in the genera *Koanophyllon*, *Decachaeta*, *Neohintonia* and *Critonia*.

Four species of *Koanophyllon* are found in Panama and two of these are endemic.

Literature:

Grashoff, J. L. & J. H. Beaman. 1970. Studies in *Eupatorium* (Compositae), III. Apparent wind pollination. Brittonia 22: 77–84.

King, R. M. & H. Robinson. 1971. Studies in the Eupatorieae (Asteraceae). LXIV. The genus, *Koanophyllon*. Phytologia 22: 147–152.

——— & ———. 1972. Studies in the Eupatorieae (Asteraceae). LXXII. Notes on the genus *Koanophyllon*. Phytologia 23: 395–396.

Robinson, B. L. 1926. *Eupatorium* L. Sp. Pl. 836. 1753. *In* P. C. Standley, Trees and Shrubs of Mexico. Contr. U. S. Natl. Herb. 23: 1432–1469.

a. Leaf blades prominently trinervate with truncate or cordate bases; inflorescence with compact cylindrical branches ..... 3. *K. solidaginoides*

aa. Leaf blades totally pinnately veined with narrowly cuneate bases; inflorescence with broadly paniculate branches.

b. Lower leaf surface with 50 or more glandular punctations per mm^2; younger stems and petioles minutely puberulous; pappus bristles narrower at the tips .... 4. *K. wetmorei*

bb. Lower leaf surface with 5–10 glandular punctations per mm^2; younger stems and

petioles coarsely hirsute; pappus bristles often as broad near the tips as at the base.

c. Heads 4–5 mm high with 8–10 florets; involucral bracts very broad, rounded to obtuse ..... 1. *K. dukei*

cc. Heads 5–6 mm high with 12–30 florets; involucral bracts narrowly ovate to lanceolate, sharply acute ..... 2. *K. panamense*

1. **Koanophyllon dukei** R. M. King & H. Robinson, Phytologia 28: 68. 1974. TYPE: Panama, Chiriquí, *Kirkbride & Duke 1038* (MO).

Shrubs to 2 m tall with few to many branches; stems with slightly fleshy surface, usually grayish, slightly wrinkled, densely and coarsely hirsute on younger parts, glabrescent. *Leaves* opposite; blades papyraceous, elliptical to broadly elliptical, 8–16 cm long and 3.3–6.3 cm wide, the base narrowly cuneate, the margins sharply serrate to serrulate, the apex narrowly short-acuminate, the surface glabrate with slightly puberulous veins, sparsely glandular-punctate below with 5–10 glands per mm^2, the secondary veins pinnate, veinlets prominently closely reticulate; petioles slender, hirsute, 1–2 cm long. *Inflorescence* pyramidal with broadly paniculate branches, the ultimate branches 1–2 mm long, densely puberulous. *Heads* 4–5 mm high with 8–10 florets; involucral bracts ca. 15, subimbricate, unequal, in 2–3 series, broadly ovate to oblong, the apex rounded to obtusely acute, the outer surface mostly 3-striate, the outer bracts more puberulous with a marginal fringe of short hairs, the inner bracts easily deciduous, reaching level of base or sometimes to middle of mature corolla; corolla greenish-white, 2.0–2.5 mm long, glabrate, with distinct cluster of capitate glands on outer surface of lobes. *Achenes* 1.3–2.3 mm long, with a few glands or bristles, the bristles mostly on upper part of ribs, the achene base narrowed with a prominent small carpopodium; pappus of ca. 30 stout closely contiguous bristles, many bristles with tips as wide as base.

Koanophyllon dukei is an endemic of the Chiriquí region in Panama. The species is distinguished from its Panamanian relatives by the smaller number of florets per head and by the broader more blunt involucral bracts. The smaller heads with fewer florets resemble those of the common *K. hylonomum* (B. L. Robinson) R. M. King & H. Robinson of Costa Rica but the latter has only minutely puberulous, less fleshy stems and dense glandular punctation on the lower leaf surface.

CHIRIQUÍ: Between Pinola and Quebrada Seco on Chiriquicito-Caldera trail, *Kirkbride & Duke 1038* (MO). Between Quebrada Seco and Quebrada nearer Caldera on Chiriquicito-Caldera trail, *Kirkbride & Duke 1008* (MO).

2. **Koanophyllon panamense** R. M. King & H. Robinson, Phytologia 28: 67. 1974. TYPE: Panama, vic. of El Valle de Antón, Coclé, *Allen 1997* (US, holotype; F, MO, isotypes).

Shrubs or small *trees* to 6 m high with few to many branches; stems with slightly fleshy surface, usually grayish, terete to slightly angular, densely and coarsely hirsute on younger parts, glabrescent. *Leaves* opposite; blades papyraceous to rather coriaceous, broadly to narrowly elliptical, mostly 12–22 cm long and 5–9 cm wide, the base narrowly cuneate, the margins serrate to serrulate,

the apex narrowly short-acuminate, the surface sparsely pilose mostly on veins, sparsely glandular-punctate below, 5–10 glands per mm^2, the secondary veins pinnate, veinlets prominently and closely reticulate; petioles often rather stout, 1–3 cm long. *Inflorescence* pyramidal, the branches broadly paniculate, the ultimate branches 2–5 mm long, laxly puberulous. *Heads* 5–6 mm high with usually 12–20 florets; involucral bracts ca. 20, subimbricate, somewhat unequal, in 2–3 series, broadly ovate to lanceolate, the apex sharply acute, the outer surface sparsely puberulous and sometimes glandular-punctate, 3–5-striate, the inner bracts easily deciduous, reaching to level of basal third or middle of mature corolla; corolla white, ca. 3 mm long, with a few capitate glands on outer surface of lobes. *Achenes* 2–3 mm long with many bristles mostly on ribs, the achene base narrow with a small short tapering carpopodium; pappus of ca. 25–30 stout closely contiguous bristles, many bristles with tips as wide as base.

Koanophyllon panamense seems related to the sympatric *K. wetmorei* by the large number of flowers per head and by the rather sharply pointed lanceolate involucral bracts. However, in the less glandular-punctate lower leaf surfaces and the stouter pappus setae, the species is more like the widely distributed *K. pittieri* (Klatt) R. M. King & H. Robinson of Mexico and Central America with which it has been confused in the past. The species differs from both relatives in the coarsely hirsute younger stems and petioles.

One specimen has been seen from Costa Rica having 15–16 florets per head and coarsely hirsute stems as in *K. panamense*. The position of the Costa Rican specimen remains unresolved because of the presence of much broader blunter involucral bracts and the presence of generally denser glandular punctations on the lower leaf surface.

BOCAS DEL TORO: Water Valley, *von Wedel 744* (MO). COCLÉ: Vic. of El Valle de Antón, 600 m, *Allen 1997* (F, MO, US). El Valle de Antón, *D'Arcy & D'Arcy 6733, 6741* (both MO). Club Campestre, ca. 700 m, *Duke 13257* (FSU, MO). Between Pilón and El Valle de Antón, 700–900 m, *Duke & Dwyer 13953* (MO). El Valle, *Dwyer 1835* (F, MO). PANAMÁ: Cerro Campana, *Croat 12073, 12159* (both MO). Cerro Campana, ca. 3000 ft, *Dwyer & Kirkbride 7858* (MO). Cerro Campana, 2700–3000 ft, *Duke 8643* (MO, OS, US). La Campana, Cerro Campana, *Ebinger 933* (MO). Cerro Campana, *Gentry 1826, 5780* (both MO). SW slopes of mtns. near Chica, *King 5335* (US). Cerro Campana, 2900 ft, *McDaniel 6868* (FSU).

3. **Koanophyllon solidaginoides** (H.B.K.) R. M. King & H. Robinson, Phytologia 22: 151. 1971.—FIG. 27.

Eupatorium solidaginoides H.B.K., Nov. Gen. Sp. Pl. 4: 99. ed. fol. 1818. TYPE: Ecuador, between Ticsan and Alausi, *Humboldt & Bonpland* (P, not seen, US, photo).
E. syringaefolium Turcz., Bull. Soc. Imp. Naturalistes Moscou 24(1): 169. 1851. TYPE: Ecuador, ravines near Ibarra, *Jameson 676* (US, isotype).
E. filicaule Shultz-Bip. ex A. Gray, Proc. Amer. Acad. Arts 21: 384. 1886. TYPE: Mexico, Tlacolula, *Ehrenberg 1176* (B, destroyed; US, isotype).
E. decussatum Klatt, Bull. Soc. Roy. Bot. Belgique 35: 295. 1896. TYPE: Costa Rica, Río Virilla, near San Juan, *Tonduz 9869* (BR).
Ophryosporus solidaginoides (H.B.K.) Hieron., Bot. Jahrb. Syst. 29: 4. 1900.
Eupatorium scoparioides L. O. Williams, Fieldiana, Bot. 36: 102. 1975. TYPE: Guatemala, Petén, abiertos de Poptún, *Molina 11595* (F, holotype; US, isotype).

Shrubs or *subshrubs* often with long arching or subscandent branches; stems

slender, to 2 m long, terete, scarcely striate, minutely puberulous. *Leaves* opposite; blades rather membranaceous, ovate, 5–12 cm long and 3–6 cm wide, the base truncate to cordate, the margins serrate-crenate, the apex caudate-acuminate, the upper surface sparsely pilose, the lower surface with numerous glandular punctations, puberulous to subtomentellous on veins, the base prominently trinervate; petioles slender, 1–2 cm long. *Inflorescence* pyramidal, the branches compact, rather spicate, the ultimate branches 1–3 mm long, densely puberulous. *Heads* 4–6 mm high with 10–15 florets; involucral bracts ca. 15, sometimes purple tinged, eximbricate, mostly subequal, in 2–3 series, narrowly oblong or lanceolate, the apex narrowly acute, the outer surface minutely puberulous and glandular-punctate, a few outer bracts more densely puberulous, the inner bracts persistent; corolla white, 2–3 mm long, with scattered capitate glands, many glands on outer surface of lobes. *Achenes* 2–3 mm long with many bristles on sides and ribs, the base narrow with a small short tapering carpopodium; pappus of ca. 30 slender scarcely contiguous bristles.

Koanophyllon solidaginoides is widely distributed from central Mexico south through Central America and the Andes to northern Peru with an isolated population in the Galapagos. The species is cited as a calciphile by B. L. Robinson in Standley (1926).

CHIRIQUÍ: Between Hato del Jobo and Cerro Vaca, 700–1000 m, *Pittier 5294* (US). PANAMÁ: Cerro Campana, ca. 750 m, *Kennedy et al. 2065* (MO).

4. **Koanophyllon wetmorei** (B. L. Robinson) R. M. King & H. Robinson, Phytologia 28: 67. 1974.

Eupatorium hypomalacum var. *wetmorei* B. L. Robinson, Contr. Gray Herb. 104: 17. 1934.
TYPE: Panama, Barro Colorado Island, *Wetmore & Abbe 77* (GH, holotype; F, isotype).

Shrubs or small *trees* 2–3 m tall with few to many branches; stems not fleshy, usually grayish-brown, terete to slightly ridged, densely minutely puberulous and sparsely glanduliferous. *Leaves* opposite; blades papyraceous, narrowly elliptical, mostly 12–20 cm long and 3.5–6.5 cm wide, the base narrowly cuneate, the margins serrulate to nearly entire, the apex slightly acuminate, long and narrow, the upper surface glabrate, the lower surface with a few hairs on veins and with many glandular punctations with 50 or more glands per mm^2, the secondary veins pinnate, the reticulations of veinlets not prominent; petioles usually slender, 1.0–3.5 cm long. *Inflorescence* pyramidal, the branches broadly paniculate, the bracts narrow or with narrow bases, the ultimate branches 1–5 mm long, minutely puberulous. *Heads* 5–6 mm high with 12–23 florets; involucral bracts ca. 20, subimbricate, unequal, in ca. 3 series, lanceolate, the apex sharply acute, the outer surface sparsely puberulous and often sparsely glandular with ca. 3 striations, the inner bracts easily deciduous, reaching to level of middle of mature corolla; corolla white, 3.0–3.5 mm long, mostly glabrous, distinct cluster of capitate glands on outer surface of lobes. *Achenes* ca. 2.5 mm long, with many short bristles on ribs and upper surfaces, the achene base narrow with small short tapering carpopodium; pappus of 27–30 contiguous bristles, the apices mostly slender.

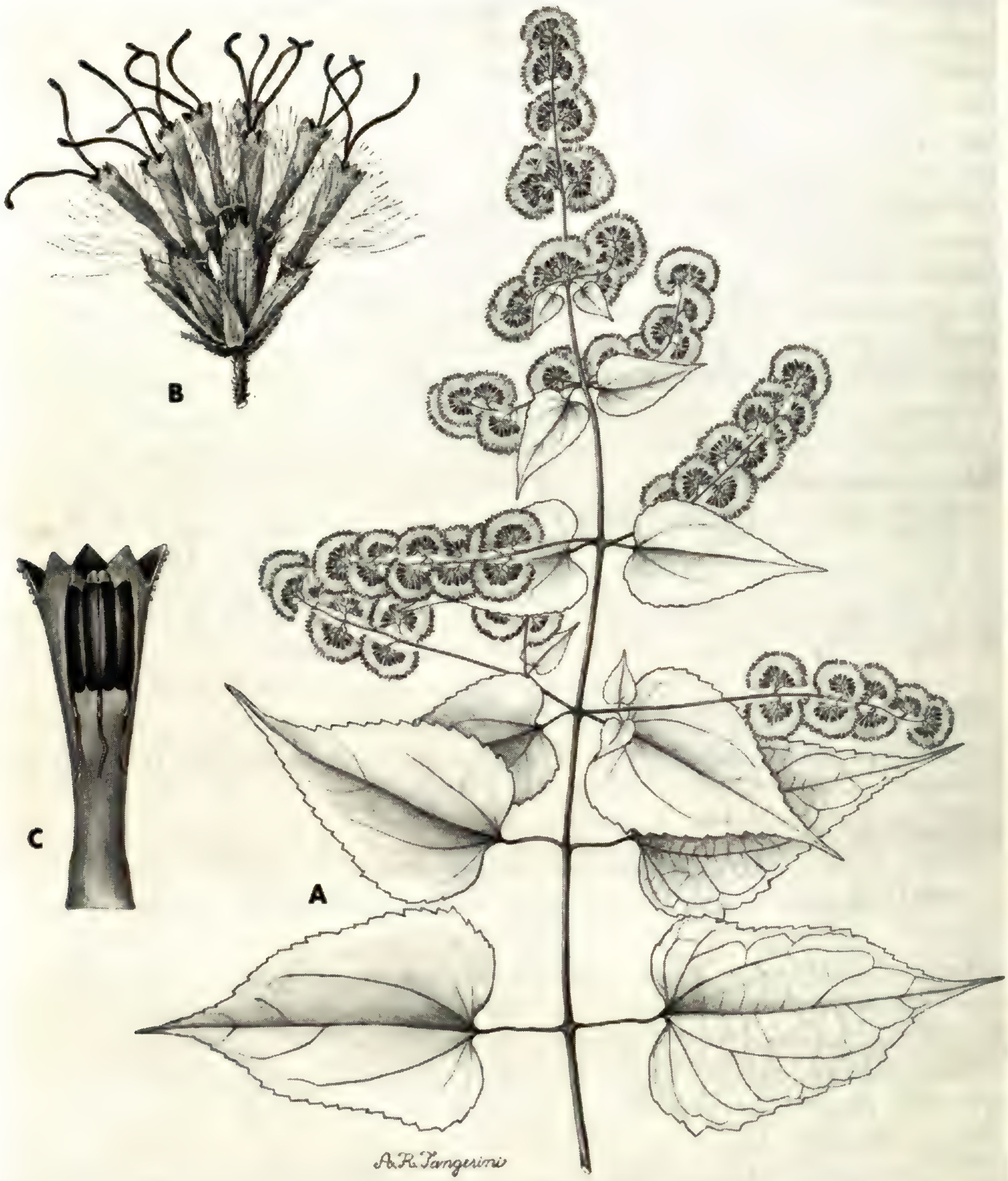

Figure 27. *Koanophyllon solidaginoides* (H.B.K.) R. M. King & H. Robinson.—A. Habit (× ½).—B. Head (× 4⅕).—C. Corolla (× 12⅗).

Koanophyllon wetmorei is known only from Panama and adjacent Costa Rica. The species was originally described as a variety of *Koanophyllon hypomalacum* (B. L. Robinson) R. M. King & H. Robinson of Guatemala, but the latter differs by the leaves having obvious short whitish puberulence below and by the bracts of the inflorescence being short with prominently enlarged carnose bases. The Panamanian material is actually more closely related to the geographically more closely associated species *K. pittieri* (Klatt) R. M. King & H. Robinson and *K.*

hylonomum (B. L. Robinson) R. M. King & H. Robinson, both occurring in Costa Rica. The relationship is particularly close to *K. hylonomum* which has similarly densely glandular-punctate lower leaf surfaces, but the latter species has smaller heads born in denser clusters, has shorter blunt involucral bracts, has only 10–11 florets per head, and has stouter pappus bristles.

A few specimens collected in southernmost Costa Rica seem to also belong to *K. wetmorei*, but these have less sharply pointed involucral bracts than the Panamanian plants.

BOCAS DEL TORO: Vic. of Chiriquí Lagoon, *von Wedel 1317* (MO). Water Valley, vic. of Chiriquí Lagoon, *von Wedel 1417* (MO). CANAL ZONE: Barro Colorado Island, *Croat 7128* (F, MO), *8144* (MO), *9554*, *13110* (both F, MO), *13273* (MO); *Brown 177* (F); *Graham 201* (MICH); *Shattuck 655* (F, MO); *Wetmore & Abbe 77* (F, GH), *87* (MO). PANAMÁ: Hills above Campana, 600–800 m, *Allen 1321* (F, MO, US).

27. MIKANIA

Mikania Willd., Sp. Pl., ed. 4. 3(3): 1742. 1803. TYPE: *Eupatorium scandens* L. typ. cons.

Carelia A. L. Jussieu ex Cav., Anales Ci. Nat. 6. 1802 (1803), not *Carelia* G. Pontedera ex P. C. Fabricius 1759. TYPE: *C. satureiaefolia* Cav. = *Mikania amara* Willd.
Corynanthelium Kunze, Linnaea 20: 19. 1847. TYPE: *C. moronoa* Kunze.
Morrenia Kunze, Linnaea 20: 1847, nom. nud. pro syn. TYPE: *M. odorata* Kunze, nom. nud.
Moronoa Kunze, error for *Morrenia*.
Willoughbya Neck. ex Kuntze, Rev. Gen. Pl. 371. 1891. TYPE: *Eupatorium scandens* L.

Vines or reclining weak *shrubs*, perennial, with few to many branches. *Leaves* opposite or rarely verticellate, distinctly petiolate; blades broadly ovate to linear, often cordate or hastate, sometimes dissected. *Inflorescence* paniculate with paniculate, racemose, spicate, corymbose or subcymose branches; pedicels present or lacking. *Heads* discoid with 4 florets; involucre of 4 subequal bracts, usually with a fifth distinct subinvolucral bract; receptacle flat, glabrous; corolla white or sometimes pink, funnelform to broadly campanulate, often with a distinct tube, 5-lobed, the lobes short to elongate, the corolla cells usually large or quadrate with straight walls, sometimes forming papillae on lower inside surface of the limb; anthers exserted, the anther collar with quadrate to short-oblong cells and inornate walls, the anther apendage as long as broad or longer; nectary usually elongate; the style base often stout, usually without a distinct enlargement, usually glabrous, sometimes papillose, the style appendages linear without enlarged tip, densely papillose, glanduliferous. *Achenes* prismatic, 4–10-ribbed, glabrous or with glands or bristles; carpopodium short-cylindrical with mostly subquadrate cells; pappus of ca. 35–60 scabrous bristles in 1–2 series, the apical cells usually blunt.

Mikania is a genus of about 300 species ranging from the eastern United States through Mexico, Central America, and the West Indies into South America. A few species are credited to the eastern hemisphere. Fourteen species have been collected in Panama. A useful treatment of *Mikania* in Venezuela is presented by Aristeguieta (1964).

Literature:

Holmes, W. C. & S. McDaniel. 1976. Notes on *Mikania* (Compositae). II. Phytologia 33: 1–3.

Robinson, B. L. 1922. II. The Mikanias of northern and western South America. Contr. Gray Herb. 64: 21–116.

———. 1934a. II. The variability of two wide-ranging species of *Mikania*. Contr. Gray Herb. 104: 49–55.

———. 1934b. III. *Mikania scandens* and its near relatives. Contr. Gray Herb. 104: 55–71.

Steyermark, J. A. 1953. Compositae. *In* Contributions to the flora of Venezuela —Botanical exploration in Venezuela III. Fieldiana, Bot. 28: 620–678.

a. Panicles with elongate racemose or spicate branches.
  b. Leaves distinctly puberulous and glandular-punctate; heads 7–9 mm high; stems never fistulose ---------- 11. *M. psilostachya*
  bb. Leaves with few hairs and not prominently glandular-punctate; heads 4–6 mm high; stems often fistulose.
    c. Heads pedicellate ---------- 6. *M. houstoniana*
    cc. Heads sessile ---------- 7. *M. leiostachya*

aa. Panicles with paniculate or corymbose branches.
  d. Stems and leaves densely villous; corollas broadly campanulate; stems never fistulose ---------- 2. *M. banisteriae*
  dd. Stems and leaves puberulous to glabrous, not densely villous; corollas broadly campanulate to narrowly funnelform; larger stems often fistulose.
    e. Leaf blades with cordate bases.
      f. Heads 8–9 mm high; corolla lobes elongate, longer than the throat ---------- 3. *M. cordifolia*
      ff. Heads 4–5 mm high; corolla lobes short, not as long as the throat.
        g. Leaves, involucral bracts, and corollas with prominent reddish glandular punctations; corollas narrowly campanulate; style base densely papillose ---------- 1. *M. amblyolepis*
        gg. Leaves, involucral bracts, and corollas with pale glands; corollas broadly campanulate; style base glabrous ---------- 9. *M. micrantha*
    ee. Leaf blades with rounded to cuneate bases.
      h. Style appendages hirsute with long papillae; style base papillose; inflorescence with regularly corymbose branches with heads almost all in groups of 3.
        i. Leaves coriaceous, bases of blades mostly rounded to slightly cuneate, lower surface with slightly reticulate veins and few hairs or glands ---------- 14. *M. zonensis*
        ii. Leaves papyraceous, bases of blades distinctly cuneate, lower surface with reticulate veins not prominent and with numerous hairs and glands ---------- 4. *M. guaco*
      hh. Style appendages not hirsute, with short papillae; style base glabrous; inflorescence without regularly corymbose branches with heads not all in groups of 3.
        j. Heads individually pedicellate; inflorescence an irregularly corymbose panicle ---------- 13. *M. tysonii*
        jj. Heads sessile in pairs or clusters; inflorescence a regular panicle with paniculate branches.
          k. Heads usually 10 or more in glomerate clusters; corollas slender below but without sharply demarcated tube ---------- 12. *M. tonduzii*
          kk. Heads in pairs or clusters of 3–5; corollas with sharply demarcated tube.
            l. Leaves oblong-ovate to oblong-lanceolate, tertiary veins closely and regularly transverse; heads ca. 5 mm high ---------- 8. *M. miconioides*
            ll. Leaves narrowly to broadly ovate, tertiary veins not in a regular transverse pattern; heads 7–9 mm high.
              m. Leaves caudate-acuminate, glabrous, with prominent included branched vein endings ---------- 10. *M. pittieri*
              mm. Leaves acute to scarcely acuminate, sparsely puberulous, included vein endings not prominent ---------- 5. *M. hookeriana*

1. **Mikania amblyolepis**[9] B. L. Robinson, Contr. Gray Herb. 61: 11. 1920. TYPE: Colombia, Bolívar, Buena Vista, *Pennell 4002* (US, isotype).

Mikania panamensis B. L. Robinson, Contr. Gray Herb. 104: 41. 1934. TYPE: Panama, around Culebra, Canal Zone, 50–150 m, *Pittier 2191* (US).

Slender, sparingly branched *vines* with numerous reddish glands on leaves, branches of inflorescence, and involucral bracts; stems yellowish to reddish, mostly terete, slightly striate, slightly puberulous, usually fistulose. *Leaves* opposite; blades broadly ovate, to 6 cm long and 4.5 cm wide, the base cordate to deeply cordate, the margins with few to many blunt dentations, the apex bluntly acute to narrowly long-acuminate, the surface glabrous except for numerous reddish glandular punctations, strongly trinervate from the base; petioles slender, 1.0–3.5 cm long. *Inflorescence* a corymbose panicle with subcymose branches, the heads often in clusters of 3; ultimate branches to 2 mm long, short-puberulous and reddish glandular-punctate. *Heads* 4.5–5.0 mm high; subinvolucral bract narrowly elliptical to lanceolate, ca. 2 mm long, the subinvolucral and outer involucral bracts puberulous and reddish glandular-punctate; involucral bracts oblong with rounded somewhat fimbriate tips, ca. 4 mm long, ca. 1 mm wide; corolla white, 2.0–2.5 mm long, the tube short, 0.5–0.8 mm long, the limb narrowly funnelform with scattered papillae on the lower inside surface, the lobes about as long as wide and partially recurved when old, the outer surface with scattered reddish glands, the corolla cells oblong, 25 μ or less wide; anther appendages firm, triangular-ovate; style bases densely papillose, the style appendages with short papillae. *Achenes* 4–5-ribbed, ca. 1.5 mm long, with many scattered yellowish glands; pappus of ca. 30 slender bristles in 1 series, the tips scarcely enlarged.

Mikania amblyolepis seems to be restricted to Panama and northern Colombia. The species can be distinguished readily from the related *M. micrantha* by the numerous reddish glandular punctations and the round-tipped involucral bracts. Other significant differences are the narrow limb of the corolla and the densely papillose base of the style.

CANAL ZONE: Around Culebra 50–150 m, *Pittier 2191* (US). Balboa, *Standley 25634, 29297, 30879* (all US). DARIÉN: Río Chico, from Yaviza at junction with Río Chucunaque to ca. 1 hour by outboard from junction, *Burch et al. 1084* (US). 0–4 mi up Río Sabana from Santa Fe, *Duke 4163* (MO). Summit Camp, between Sasardí and Mortí, ca. 400 m, *Duke 10035* (MO, FSU). Río Sabana, ca. 4 mi above Santa Fe, ca. 25 m, *Duke 10214* (MO, OS). 2 mi E of Santa Fe, *Tyson et al. 4820* (MO). PANAMÁ: 5–6 mi E of Chepo, *Duke 4053* (MO). Sabanas near Chepo, 30 m, *Hunter & Allen 50* (MO). Pearl Island, *Johansen 115* (US). SAN BLAS: Sasardí, ca. 20 m, *Duke 10130* (MO, OS). Eslogandi, ca. 200 m, *Duke 10194* (MO, OS).

2. **Mikania banisteriae** DC., Prodr. 5: 193. 1836. TYPE: Brasil, *Poeppig 135* (G-DC, holotype, not seen, US, microfiche; F, isotype not seen, US, photo).—FIG. 28.

M. ruiziana Poepp. in Poepp. & Endlich., Nov. Gen. Sp. Pl. 3: 53. 1845. TYPE: Peru, Cuchero, *Poeppig 1473* (W, not seen; B, destroyed, US, photo)

M. caudata Benth., Pl. Hartw. 201. 1845. TYPE: Colombia, in sylvis prope Guaduas, Bogotá, *Hartweg 1112* (K, not seen).

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[9] W. C. Holmes, Mississippi State University is credited for pointing out the priority of this name.

M. ruiziana Poepp. var. *lehmanniana* Hieron., Bot. Jahrb. Syst. 19: 45. 1894. TYPE: Colombia, near Dolores, Tolima, 1000–1800 m, *Lehmann 7483* (K, not seen; F, not seen, US, photo).
Willoughbya ferruginea Rusby, Mem. Torrey Bot. Club 6: 58. 1896. TYPE: Bolivia, Guanai-Tipuani, *Bang 1419* (NY, holotype, not seen; US, isotype).
Mikania antioquiensis Hieron., Bot. Jahrb. Syst. 28: 580. 1901. TYPE: Colombia, prope Santa Domingo, Cancan et Amalfi, 1500–2000 m, *Lehmann 7971* (US).
M. antioquiensis Hieron. var. *subcuneata* B. L. Robinson, Contr. Gray Herb. 104: 32. 1934. TYPE: Peru, Iquitos, trail to San Juan, Loreto, *Mexia 6492* (US).
M. ferruginea Rusby var. *subglabra* B. L. Robinson, Contr. Gray Herb. 104: 36. 1934. TYPE: Bolivia, San Carlos, Mapiri, *Buchtien 1576* (US).
M. almagroi Cuatr., Anales Univ. Madrid 4, fasc. 2: 233. 1935. TYPE: Ecuador, San José, *Isern 368* (MA, not seen).
M. skutchii Blake, Brittonia 2: 333. 1937. TYPE: Costa Rica, El General, 1130 m, *Skutch 2514* (US).
M. canaquensis Badillo, Bol. Soc. Venez. Ci. Nat. 9: 132. 1944. TYPE: Venezuela, Canaguá, Mérida, *Badillo 562* (VEN).
M. molinensis Badillo, Bol. Soc. Venez. Ci. Nat. 10: 296. 1946. TYPE: Venezuela, near El Molino, between Canaguá and Sta. Cruz de Mora, Mérida, *Badillo 610* (VEN).
M. oniaensis Badillo, Bol. Soc. Venez. Ci. Nat. 10: 297. 1946. TYPE: Venezuela, along Río Onia, near Bolero, N of Mesa Bolívar, Mérida, *Steyermark 56736* (VEN).
M. kavanayensis Badillo, Bol. Soc. Venez. Ci. Nat. 10: 300. 1946. TYPE: Venezuela, Gran Sabana, between Mission of Santa Teresita de Kavanayén NW to Río Karuai, Bolívar, *Steyermark 59374* (VEN, photo US).
M. ptaretepuiensis Badillo, Bol. Soc. Venez. Ci. Nat. 10: 302. 1946. TYPE: Venezuela, Petare-tepuí, Bolívar, *Steyermark 59936* (VEN).
M. meridana Badillo, Bol. Soc. Venez. Ci. Nat. 10: 303. 1946. TYPE: Venezuela, Montaña de San Jacinto, Mérida, *Steyermark 56667* (VEN).
M. bergantinensis Badillo, Bol. Soc. Venez. Ci. Nat. 10: 304. 1946. TYPE: Venezuela, Cerro San José, between Bergantín and Cerro Peonía, Anzoátegui, *Steyermark 61540* (VEN).
M. banisteriae DC. f. *lehmanniana* (Hieron.) Steyerm., Fieldiana, Bot. 28: 657. 1953.
M. banisteriae DC. f. *subglabra* (B. L. Robinson) Steyerm., Fieldiana, Bot. 28: 657. 1953.

Coarse *vines* with few branches; stems and leaves densely yellowish-villous; stems brownish, terete, striate, not fistulose. *Leaves* opposite; blades broadly ovate to ovate-lanceolate, to 18 cm long and 10 cm wide, the base rounded to cordate, the margins entire or with remote denticulations, the apex acute to narrowly short-acuminate, the surface densely villous with stout hairs, without glandular punctations, pairs of secondary veins prominent near the base and near the basal fourth; petioles rather stout, to 2 cm long. *Inflorescence* a pyramidal panicle with paniculate branches, the ultimate branches 1–4 mm long, densely hirtellous. *Heads* 7–9 mm high; subinvolucral bract ovate to obovate, 2.5–4.0 mm long with few to many abaxial hairs; involucral bracts broadly oblong with rounded tips, 3–5 mm long and 1 mm wide, glabrate; corolla whitish or pinkish, 4.5–5.0 mm long, the tube 2 mm long, the limb abruptly broadly campanulate, the lobes triangular, 1.0–1.5 mm long, 0.7–1.0 mm wide, with a few apical hairs; anther appendanges firm, oblong-ovate, 1½ times as long as wide; style base slightly thickened, glabrous, the style appendages with only short papillae. *Achenes* with 5 ribs, 3–4 mm long, with a few long hairs along the costae, the base of achene

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FIGURE 28. *Mikania banisteriae* DC.—A. Habit (× ½).—B. Heads (× 2⅘).—C. Florets (× 3⁹⁄₁₀).—D. Subinvolucral bract (× 3³⁄₁₀).—E. Nectary and base of style (× 8³⁄₁₀).—F. Stamens (× 33).—G. Achene cross section (× 11¹⁄₁₀).—H. Head cross section (× 5⅗).—I. Pappus bristle (× 11¹⁄₁₀). [After Martius, Flora Brasiliensis 6(2): plate 71. 1876.]

A
B
C
D
E
F
G
H
I

slightly attenuated; carpopodium small; pappus of ca. 35–50 slender bristles, the tips of the bristles often slightly enlarged.

Mikania banisteriae is widely distributed from Costa Rica to the Amazon Basin of Brazil and reaches south to Bolivia. Many variations have been named as distinct species. The present broad concept follows mostly that of Steyermark (1953) with the exclusion of *M. monagasensis* Badillo of Venezuela (see Aristeguieta, 1964) and *M. lanuginosa* DC. of southeastern Brazil, and with the inclusion of *M. skutchii* Blake of Costa Rica. The excluded species listed above, as well as *M. eriophora* Schultz-Bip. and the doubtfully distinct *M. pyramidata* D.Sm. both of Mexico and northern Central America, can be distinguished from *M. banisteriae* by the leaves being distinctly trinervate from at or very near the base of the blade. In *M. banisteriae* the leaves are less strongly trinervate from higher on the blade, nearer the basal fourth.

PANAMÁ: Past Cerro Jefe toward La Eneida, *Croat 13095* (MO). Cerro Azul, *Duke 9380* (MO, US). Cerro Jefe, *Dwyer 8494* (MO). Cerro Jefe, 2700–3000 ft, *Tyson et al. 3277* (MO). VERAGUAS: 5 mi NW of Santa Fe, 700–1200 m, *Croat 23191* (MO).

3. **Mikania cordifolia** (L.f.) Willd., Sp. Pl., ed. 3. 1746. 1804.

Cacalia cordifolia L.f., Suppl. Pl. 351. 1781. TYPE: Colombia, *Mutis 1818* (US).
Mikania mollis H.B.K., Nov. Gen. Sp. Pl. 4: 105. ed. fol. 1818. TYPE: Peru, Guancabamba River, *Humboldt & Bonpland* (P. not seen, US, microfiche).
M. suaveolens H.B.K., Nov. Gen. Sp. Pl. 4: 106. ed. fol. 1818. TYPE: Colombia, near Guaruma, *Humboldt & Bonpland* (P, not seen, US, microfiche).
M. poeppigii Spreng., Syst. Veg. 3: 422. 1826. TYPE: Cuba, *Poeppig* (P?, not seen; W?, not seen).
M. gonoclada DC., Prodr. 5: 199. 1836. TYPE: Mexico, Tampico, Tamaulipas, *Berlandier 137* (G-DC, not seen, US, microfiche).
M. convolvulacea DC., Prodr. 5: 199. 1836. TYPE: Santo Domingo, *Poiteau* (G-DC, not seen, US, microfiche).
Eupatorium marquezianum Gomez de la Maza, Dicc. Bot. Nom. Vulgares Cubanos & Puerto-Riquenos 54. 1889, new name for *Mikania mollis* H.B.K., not *Eupatorium molle* H.B.K.
Willoughbya cordifolia (L.f.) Kuntze, Rev. Gen. Pl. 1: 372. 1891.

Slender sparingly branched *vines*; stems yellowish-green to brownish, rather hexagonal, slightly striate, glabrate to minutely puberulous, the larger stems sometimes fistulose. *Leaves* opposite; blades broadly ovate 5–15 cm long and 3–12 cm wide, the base cordate to deeply cordate, the margins subentire to coarsely and bluntly dentate, the apex usually distinctly short-acuminate, the surface densely short-puberulous to glabrate with distinct glandular punctations below, the venation strongly trinervate from base; petioles slender, 2.0–5.5 cm long. *Inflorescence* a corymbose panicle with subcymose branches; heads often in clusters of 3; ultimate branches to 3 mm long, puberulous to glabrate. *Heads* ca. 8–9 mm high; subinvolucral bract broadly elliptical to obovate, 3.0–4.5 mm long, acute to short-acuminate, sparsely to densely puberulous; involucral bracts oblong-lanceolate with short to long-acute tips, 6–7 mm long, ca. 1 mm wide, the outer pair usually distinctly puberulous; corolla white, ca. 4 mm long, the tube narrow, 1.5–2.0 mm long, the limb narrowly campanulate, cleft to about middle into narrow lobes, scattered glands on outer surface, few to many papillae on the lower surface within, cells subquadrate and ca. 25 μ wide; anther appendages firm,

triangular, about twice as long as wide; style base glabrous, the style appendage with short papillae. *Achenes* 5-ribbed, 1.5–2.0 mm long, the sides sparsely puberulous; pappus of 50–60 slender bristles mostly in 1 series, slightly enlarged apically.

Mikania cordifolia is a widely distributed species ranging from the southern United States through Mexico, Central America, and the West Indies into South America. The species seems superficially just an enlarged form of *M. micrantha*. In addition to the size of the heads, however, *M. cordifolia* differs by the more hexagonal somewhat less fistulose stems, by the usually more pubescent subinvolucral bracts, by the narrower limb of the corolla, and by the deeply cut, elongate corolla lobes.

CANAL ZONE: Chagres, *Fendler 151* (MO, US). Las Cruces Trail, 75 m, *Hunter & Allen 704* (MO). Near old Fort Lorenzo, mouth of Río Chagres, *Piper 5903* (US). CHIRIQUÍ: Cerro Respinga above town of Cerro Punta, 8400 ft, *D'Arcy & D'Arcy 6564* (MO). Palo Santo, 3 mi N of Volcán, *Croat 13579* (MO). Boquete, Cerro Horqueta, 5000–6000 ft, *Dwyer & Hayden 7689* (MO, REED, US). Burica Peninsula, 6 km W of the airport of Puerto Armuelles, 100–200 m, *Liesner 3* (MO). COCLÉ: Near La Mesa, *Croat 13363* (MO). DARIÉN: Agua Fria, ca. 8 mi N of Santa Fe, ca. 50 m, *Duke 10114* (MO, OS). PANAMÁ: San José Island, *Johnston 1348* (MO, US). Pearl Islands, Trapiche Island, *Miller 1884* (US). Punta Paitilla, *Standley 30803* (US).

4. **Mikania guaco** H. & B., Pl. Aeq. 2: 84. 1809. TYPE: Colombia, Magdalena River between Mahates & Angostura, *Humboldt & Bonpland* (P, not seen, US, microfiche).

M. amara var. *guaco* (H. & B.) Baker in Mart., Fl. Bras. 6(2): 237. 1876.
Willoughbya guaco (H. & B.) Kuntze, Rev. Gen. Pl. 1: 372. 1891.
Mikania olivacea Klatt, Bull. Soc. Roy. Bot. Belgique 31: 195. 1892 (1893). TYPE: Costa Rica, foréts de Buenos-Aires, 2300 m, *Pittier 4433* (BR?, not seen; GH?, not seen).

Coarse sparingly branched *vines*; stems mostly brownish, terete, striate, glabrate, usually fistulose. *Leaves* opposite; blades broadly ovate, to 25 cm long and 15 cm wide, the base short-acute to acuminate, the margins entire, the apex broadly to narrowly short-acuminate, the upper surface sparsely puberulous and with minute spicules, the lower surface rather densely short-puberulous with numerous yellowish glandular punctations, the veins mostly pinnate; petioles slender, to 4.5 cm long. *Inflorescence* rather densely corymbose with almost all heads in clusters of 3, the ultimate branches ca. 0–1 mm long. *Heads* ca. 8–10 mm high; subinvolucral bract linear-lanceolate, to 2 mm long, short-puberulous; involucral bracts oblong with rounded tips, 5–6 mm long, ca. 1 mm wide, the outer pair puberulous; corolla whitish, ca. 6 mm long, the tube narrow, 2.5–3.0 mm long, the limb narrowly funnelform, the lobes short-triangular, about as long as wide, with scattered slender hairs on the outer surface, the cells subquadrate and ca. 25 μ wide; anther appendages firm, triangular, about twice as long as wide; style base slender, usually sparsely papillose, the style appendages hirsute with many long papillae. *Achenes* with 5 ribs or grooves, thickly corticated and terete when fully mature, ca. 4 mm long, the sides sparsely puberulous; pappus of ca. 50 slender bristles which are not or only slightly enlarged apically.

Mikania guaco is widely distributed in tropical America from Mexico to Brazil and is the most common representative of a group that has heads almost all in

groups of 3–5, style branches hirsute with long papillae, and achenes highly corticated when fully mature. A close relative, *M. parviflora* (Aubl.) Karst., distinguished by its broad subinvolucral bracts, seems to occur as close to Panama as the Chocó in Colombia. More distant geographically is *M. trinitaria* DC. of Venezuela, Guayana, and adjacent Brazil. The latter has large bracts as in *M. parviflora*, but also has a deeply cleft corolla with long narrow lobes.

BOCAS DEL TORO: Vic. of Chiriquí Lagoon, Bustimentos "lighthouse," *von Wedel 2920* (MO, US). CANAL ZONE: Chagres, *Fendler 153* (MO, US). Vic. of Fort Sherman, *Standley 30989* (US). CHIRIQUÍ: Trail from Paso Ancho to Monte Lirio, upper valley of Río Chiriquí Viejo, 1500–2000 m, *Allen 1578* (MO, US). 1 mi E of Cañas Gordas, near Costa Rican Border, 800–1200 m, *Liesner 281* (MO). Pastures around El Boquete, 1000–1300 m, *Pittier 2996* (US). DARIÉN: Río Sambú, 0.5 mi above Río Venado, *Duke 9292* (MO, OS, US). Asnati, 200–300 m, *Duke 10050* (MO). Helipad, Camp Cañasas, Upper Río Sabana tributary, 312 ft, *Duke 15547* (OS, REED). Along the Sambú River, *Pittier 5544* (US). PANAMÁ: San José Island, *Johnston 1372* (MO, US), *1279* (US), *1319* (MO, US). Cerro Campana, 2700 ft, *McDaniel 6901* (FSU, MO).

5. **Mikania hookeriana** DC., Prodr. 5: 195. 1836. TYPE: British Guiana, *Schomburgk*? (K, not seen; G-DC fragment, not seen, US, microfiche).

M. badieri DC., Prodr. 5: 194. 1836. TYPE: Guadeloupe, *Badier* (G-DC, not seen, US, photo).
M. platyphylla DC., Prodr. 5: 195. 1936. TYPE: Peru, *Poeppig* (G-DC, not seen, US, microfiche).
M. gracilis Schultz-Bip. ex Miq., Stirp. Surinam. Sel. 187. 1850. TYPE: Surinam, *Hostmann & Kappler 1017* (G, MO, not seen, US, photos).
M. imrayana Griseb., Fl. Brit. W. Ind. 363. 1861. TYPE: Dominica, *Imray* (K, not seen).
Willoughbya imrayana (Griseb.) Kuntze, Rev. Gen. Pl. 1: 372. 1891.
W. platyphylla (DC.) Kuntze, Rev. Gen. Pl. 1: 372. 1891.
Mikania badieri DC. var. *kittsiana* Urb., Symb. Antil. 5: 220. 1907. TYPE: St. Kitts, Belmont, *Britton & Cowell 385* (US).
M. vitrea B. L. Robinson, Contr. Gray Herb. 61: 22. 1920. TYPE: Venezuela, Colonia Tovar, Aragua, *Fendler 2349* (GH, not seen; G not seen, US, photo).
M. hookeriana DC. var. *badieri* (DC.) B. L. Robinson, Contr. Gray Herb. 104: 52. 1934.
M. hookeriana DC. var. *kittsiana* (Urb.) B. L. Robinson, Contr. Gray Herb. 104: 52. 1934.
M. hookeriana DC. var. *platyphylla* (DC.) B. L. Robinson, Contr. Gray Herb. 104: 52. 1934.
M. hookeriana DC. var. *cardiophylla* B. L. Robinson, Contr. Gray Herb. 104: 53. 1934. TYPE: Lesser Antilles, St. Vincent, *H. H. & G. W. Smith 1890* (GH, not seen).
M. hookeriana DC. var. *crassicaulis* Steyerm., Fieldiana, Bot. 28: 658. 1953. TYPE: Venezuela, Ptari-tepui, Bolívar, *Steyermark 60015* (F, not seen).
M. sanjacimtensis Badillo, Bol. Soc. Venez. Ci. Nat. 10: 298. 1946. TYPE: Venezuela, Montaña de San Jacinto, N side of Río Chama, Mérida, *Steyermark 56665* (VEN).

Coarse usually woody, sparingly branched *vines*; stems pale to dark brownish, terete, striate, slightly puberulous to sparsely hirsute, the larger stems often fistulose. *Leaves* opposite; blades usually ovate to broadly ovate, sometimes with prominent angles, to 15 cm long and 10 cm wide, the base rounded, the margins entire, the apex short-acute to slightly acuminate, the upper surface sparsely puberulous to glabrate, the lower surface brownish puberulous, glandular punctations not prominent, the venation with two pairs of prominent secondary veins in the basal quarter, the upper pair strongly ascending and giving a trinervate aspect, the tertiary veins not prominently and regularly transverse; petioles sometimes slender, 1–5 cm long. *Inflorescence* a panicle with paniculate branches, the branches puberulous; heads in pairs or groups of 3 congested near tips of short branches, sessile. *Heads* 8–9 mm high; subinvolucral bract 1.5–2.0 mm long,

thin with few or no hairs abaxially; involucral bracts oblong with rounded tips, ca. 4 mm long including the somewhat swollen bases, ca. 1 mm wide, somewhat puberulous and glandular-punctate on outer surface; corolla whitish, fragrant, 4.5–5.5 mm long, the tube distinct, 1.0–1.5 mm long, the limb narrowly campanulate, the lobes half again as long as wide with a few glands and short hairs near the tips, the cells oblong, 15–25 μ wide, the cell walls slightly sinuous; anther appendages firm, ovate-triangular, slightly longer than wide; style base glabrous, the style appendages with short papillae. *Achenes* with 4–5 ribs, ca. 3.5 mm long, the sides with a few short hairs and glands; pappus of 40–50 slender, sometimes sharply angled, bristles mostly in 1 series, the tips not or scarcely enlarged, the apical cells often acute.

Mikania hookeriana is distributed from southern Mexico south to Peru and Brazil. The sessile heads are one of the distinctive features of the species. The extensive synonymy of the species is discussed by B. L. Robinson (1934a). Also discussed by Robinson is the superficially similar and widely distributed *M. vitifolia* DC. The latter species differs most obviously by the pedicellate heads and the more acuminate and glandular-punctate leaves. Another species, *M. angularis* H. & B. of northern South America, is very close to *M. vitifolia* but has much longer corolla lobes. No specimens of *M. vitifolia* or *M. angularis* are known from Panama.

CANAL ZONE: Barro Colorado Island, *Bangham 597* (US). Pipeline Road, *Gentry 1794* (MO). COCLÉ: Hills N of El Valle de Antón, trail to La Mesa, ca. 1000 m, *Allen 2688* (MO, US). Hills above El Valle de Antón, *D'Arcy & D'Arcy 6753* (MO). COLÓN: Vic. of Camp Piña, 25 m, *Allen 3671* (MO). Summit of Cerro Santa Rita, 1200–1500 ft, *Allen & Allen 5098* (MO). PANAMÁ: 7 mi N of Cerro Azul on the road to Cerro Jefe, 2600 ft, *Blum et al. 1764* (MO, US). 3 mi above Interam. Hwy. on road to Cerro Campana, *Croat 12055* (MO). Approach to Cerro Jefe, *Croat 15239* (MO). Cerro Jefe, *Duke 9446* (MO, REED). Cerro Azul, *Dwyer 2797A* (MO, US). La Campana, Cerro Campana, *Ebinger 940* (MO, US). Cerro Jefe, 2.5 mi beyond Finca Indio, *Gentry 2125* (MO). Cerro Campana, ca. 1000 m, *Gentry 5763* (MO). Near Cerro Campana, *Kirkbride & Hayden 300* (MO). Cerro Campana, 2800 ft, *McDaniel 6832* (FSU, MO). Cerro Azul, *Porter et al. 4151* (MO). E slope of Cerro Jefe, 2700–3000 ft, *Tyson et al. 3338* (MO). Cerro Azul to Cerro Jefe, *Tyson et al. 4324* (MO). Slopes of Cerro Jefe beyond Cerro Azul, *Wilbur & Wilbur 11366* (MO).

6. **Mikania houstoniana** (L.) B. L. Robinson, Proc. Amer. Acad. Arts 42: 47. 1906.

Eupatorium houstonianum L., Sp. Pl. 836. 1753. TYPE: Mexico, Veracruz, *Houston* (BM).
E. houstonis L., Syst. Nat., ed. 10. 1204. 1759. Citation including same description as in Hortus Cliffortianus and evidently a variant of the above name based on the same type.
E. fruticosum Mill., Gard. Dict., ed. 8. 1768. (*Eupatorium* no. 6). TYPE: Cultivated, seed from Veracruz, Mexico, *Houston* (BM, not seen).
Mikania houstonis (L.) Willd., Sp. Pl. 3: 1742. 1803.
Willoughbya houstonis (L.) Kuntze, Rev. Gen. Pl. 1: 373. 1891.

Coarsely herbaceous sparingly branched *vines*; stems yellowish to brown, terete, striate, glabrate to spreading-pubescent, the larger stems usually fistulose. *Leaves* opposite; blades ovate, to 13 cm long and 10 cm wide, the base rounded to slightly cuneate, the margins entire, the apex usually somewhat abruptly short-acuminate, the surface glabrate, obscurely glandular-punctulate beneath, 2–3 pairs of prominent secondary veins arching outward and upward from the basal fifth of

the blade, the tertiary veins sometimes regularly transverse, prominent beneath; petioles slender, 1–4 cm long. *Inflorescence* a panicle with elongate strictly racemose branches, the ultimate branches 1–3 mm long arising from axils of subinvolucral bracts. *Heads* 4–6 mm high; subinvolucral bract ovate-lanceolate, 1.5–2.0 mm long, minutely puberulous; involucral bracts oblong with rounded tips, 3.0–4.5 mm long, ca. 0.8 mm wide, the outer pair minutely puberulous; corolla white, fragrant, 2.5–3.0 mm long, the tube narrow, ca. 1.5 mm long, the limb narrowly campanulate with prominent undulations on the lower inside surface, the lobes about as long as wide with few glands outside, the cells of the corolla oblong, 15–20 μ wide, mostly with sinuous walls; anther appendages firm, ovate, ca. 1½ times as long as wide; style base thickened, glabrous, the style appendages with short papillae. *Achenes* with 5 ribs, ca. 2 mm long, glabrous; pappus of ca. 35–40 slender bristles mostly in 1 series, the apices slightly enlarged.

Mikania houstoniana is distributed from Mexico southward to Bolivia. The racemose branches of the inflorescence with short pedicels from the axils of sessile bracts are a distinctive feature of the species. This species and the closely related *M. leiostachya* Benth. have narrow and sinuous-walled cells in the corolla that are rather unusual in the genus.

BOCAS DEL TORO: Bocas del Toro, *Dunlap 168* (US).

7. **Mikania leiostachya** Benth., Pl. Hartw. 201. 1845. TYPE: Colombia, in descensu a Guaduas ad Honda, Prov. Bogotá, *Hartweg 1110* (K, not seen).

Coarsely herbaceous sparingly branched *vines*; stems yellowish to brown, terete, striate, glabrate to minutely puberulous, the larger stems usually fistulose. *Leaves* opposite; blades ovate, to 18 cm long and 11 cm wide, the base rounded to slightly cordate, the margins entire and slightly recurved, the apex abruptly shortly caudate-acuminate, the upper surface glabrate, the lower surface short-puberulous, without evident glandular-punctations, 2–3 pairs of prominent secondary veins arching outward and upward from basal fifth of the blade, the tertiary veins regularly transverse, prominent beneath; petioles slender, 1–3 cm long. *Inflorescence* a panicle with elongate strictly spicate branches. *Heads* 5–6 mm high; subinvolucral bract ovate, acute, ca. 1.5 mm long, minutely puberulous; involucral bracts oblong with rounded tips, 3.0–3.5 mm long, ca. 0.8 mm wide, the outer pair minutely puberulous; corolla white, fragrant, 2.5–3.0 mm long, the tube narrow, 1.0–1.5 mm long, the limb narrowly campanulate with prominent undulations on the lower inside surface, the lobes 1–2 times as long as wide with a few glands outside, the corolla cells oblong, 15–25 μ wide, mostly with sinuous walls; anther appendages firm, ovate, ca. 1½ times as long as wide; style base somewhat thickened, glabrous, the style appendages with short papillae. *Achenes* with 5 ribs, 1.5–2.0 mm long, glabrous; pappus of 35–40 slender bristles in 1 series, the apices slightly to distinctly thickened.

Mikania leiostachya is known from Central America and northern South America. The species is most distinctive in the strictly spiciform branches of the inflorescence. The sessile heads seem to be the only constant difference from the widely distributed *M. houstoniana* (L.) B. L. Robinson.

CANAL ZONE: Barro Colorado Island, *Croat 7687, 7850, 13245, 13494* (all MO). Madden Forest Road 1, *Croat 8947* (MO). 2 mi NE of Summit Gardens, *Croat 13795* (MO). Fort Sherman: U.S. Army Tropic Test Center Site, Skunk Hollow, *Dwyer & Robyns 145* (MO, US). Barro Colorado Island, *Foster 1467* (MO), *2176* (US). Gatún Station, *Hayes 309* (MO, US). Valley of Masambi, on the road to Las Casadas Plantation, 20–100 m, *Pittier 2671* (US). Barro Colorado Island, *Woodworth & Vestal 558* (MO). COLÓN: Lagarto, *Cowell 256* (US). PANAMÁ: San José Island, *Johnston 1329* (MO, US). Río Tocumen, *Standley 29387* (US).

8. **Mikania miconioides** B. L. Robinson, Contr. Gray Herb. 61: 19. 1920. TYPE: Colombia, Santa Marta, *Smith 631* (US, isotype).

Slightly woody, sparingly branched *vines*; stems yellowish to brown, terete to slightly hexagonal, striate, minutely puberulous, the larger stems usually fistulose. *Leaves* opposite; blades elliptical to oblong-lanceolate, to 19 cm long and 8 cm wide, the base short-acute, the margins entire to remotely serrulate, the apex abruptly short caudate-acuminate, the surface minutely puberulous or with scattered minute glandular punctations, 2 pairs of prominent subparallel secondary veins in basal fourth of blade strongly ascending and reaching almost to leaf tip, the bases of the veins more widely separated in more oblong leaves, the tertiary veins prominent and mostly transverse, often close; petioles 1–3 cm long. *Inflorescence* a panicle with paniculate puberulous branches. *Heads* usually in somewhat isolated pairs or in spreading apical groups of 3, mostly sessile, ca. 5 mm high; subinvolucral bract minute, ca. 0.5 mm long; involucral bracts oblong with broadly rounded tips, 3.0–3.5 mm long including slightly swollen bases, ca. 1 mm wide, distinctly puberulous and with pale glandular punctations; corolla whitish, 3.0–3.5 mm long, the tube distinct, 1.0–1.3 mm long, the limb narrowly campanulate, cleft ¼–⅓ into short lobes, the outer surface with a few hairs or glands, the corolla cells oblong, 15–25 μ wide; anther appendages often thin, slightly longer than wide; style base glabrous, the style appendages with short papillae. *Achenes* 5-ribbed, 1.5–2.0 mm long, glabrous or with a few hairs or bristles near the top; pappus of ca. 30–35 slender flattened bristles in 1 series, the tips distinctly enlarged.

Mikania miconioides is known from Colombia, Panama, and Costa Rica. The species is most closely related to *M. sylvatica* Klatt of northern South America, but the latter has more coriaceous leaves with much shorter petioles and scarcely acuminate tips. The upper leaf surface also has the main veins more depressed.

BOCAS DEL TORO: N slopes of Cerro Horqueta, 6000–7000 ft, *Allen 4926* (MO). CHIRIQUÍ: Cerro Horqueta, *Blum 700* (MO). Cerro Horqueta, 7000 ft, *Blum & Dwyer 2625* (MO). Boquete, Cerro Horqueta, 5000–6000 ft, *Dwyer & Hayden 7705* (MO). Cerro Campana, *Gentry 5782* (MO).

9. **Mikania micrantha** H.B.K., Nov. Gen. Sp. Pl. 4: 105. ed. fol. 1818. TYPE: Venezuela, near Caripe Cumanensium, *Humboldt & Bonpland* (P, not seen, US, microfiche).

M. orinocensis H.B.K., Nov. Gen. Sp. Pl. 4: 105. ed. fol. 1818. TYPE: Venezuela, Insulae Pararuma (Missiones del Orinoco), *Humboldt & Bonpland* (P, not seen, US, microfiche).
M. subcrenata Hook. & Arn., Companion Bot. Mag. 1: 243. 1836. TYPE: Argentina, woods of Tucumán, *Tweedie 1189* (K, not seen).
M. umbellifera Gardn., London Jour. Bot. 4: 119. 1845. TYPE: Brasil, Organ Mts., ca. 4000 ft, *Gardner 483* (BM, not seen).

M. subcymosa Gardn., London Jour. Bot. 6: 448. 1847. TYPE: Brasil, Goyaz, *Gardner 3271* (US).
M. sinuata Rusby, Bull. New York Bot. Gard. 8: 127. 1912. TYPE: Bolivia, San Juan, *Williams 207* (US).

Slender, sparingly branched *vines*; stems yellowish or brownish, terete to slightly 4-angled, slightly striate, glabrate to sparsely puberulous, mostly fistulose. *Leaves* opposite; blades ovate, 3–13 cm long and to 10 cm wide, the base cordate to deeply cordate, the margins subentire to coarsely dentate, the apex narrowly short-acuminate, the surface glabrate with numerous pale glandular punctations, strongly trinervate from the base; petioles slender, 1–6 cm long. *Inflorescence* a corymbose panicle with subcymose branches, heads often in clusters of 3; ultimate branches up to 2 mm long, usually glabrous. *Heads* 4–5 mm high; subinvolucral bract narrowly elliptical to narrowly obovate, ca. 2 mm long, short-acuminate, glabrous to short-puberulous; involucral bracts oblong with short-acuminate tips, ca. 3.5 mm long, ca. 1 mm wide, glabrous to short-puberulous; corolla white, 2.5–3.0 mm long, the tube narrow, 1.0–1.3 mm long, the limb broadly campanulate with partially to fully developed ridges of papillae inside, the lobes about as long as wide and strongly recurved when old, the outer surface with a few pale glands, the corolla cells mostly quadrate and less than 25 μ wide; anther appendages firm, triangular-ovate; style base glabrous, the style appendages with short papillae. *Achenes* 4–5-ribbed, 1.5–2.0 mm long with many scattered pale glands; pappus of 35–40 slender bristles mostly in 1 series, the tips usually slightly enlarged.

Mikania micrantha occurs in Mexico, Central America, the West Indies, and northern South America. The species is the most widely distributed member of the genus with representatives or close relatives as far away as Africa. The close relationship to *M. scandens* (L.) Willd. of the eastern United States has been discussed by B. L. Robinson (1934b), and the often colored corollas with less reflexed lobes of the latter species have been noted. Most of the subtle distinctions mentioned by B. L. Robinson seem to be derived from the larger cells in the corollae of *M. scandens*, these cells often being oblong and over 25 μ wide. Papillae on the inner surface of the corolla limb and enlarged tips on the pappus bristles are also rarer in *M. scandens*.

BOCAS DEL TORO: Santa Catalina, *Blackwell et al. 2720* (MO). Bocas del Toro, *Carleton 77* (US). Almirante, *Cooper 148* (US). Changuinola Valley, *Dunlap 257* (US). Hill side above Almirante, *Gentry 2699* (MO). Bocas del Toro, *Lazor et al. 2392* (MO). Water Valley, *von Wedel 592, 869* (both MO). Vic. of Chiriquí, *von Wedel 1283* (MO, US). Water Valley, vic. of Chiriquí Lagoon, *von Wedel 1713* (MO, US). Old Bank Island, vic. of Chiriquí Lagoon, *von Wedel 1897* (MO, US). Isla Colón, vic. of Chiriquí Lagoon, *von Wedel 2474* (MO, US). Shephead Island, vic. of Chiriquí Lagoon, *von Wedel 2680* (MO). Johns Creek, vic. of Chiriquí, *von Wedel 2771* (MO, US). Bocas del Toro, *Wedel 329* (MO). CANAL ZONE: Barro Colorado Island, *Aviles 6* (MO). France Field, *Blum & Dwyer 2122* (MO). Gamboa, *Heriberto 43* (US). Río Chagres, Gatún Dam, 0–5 m, *Busey & Mahler 341* (MO). Barro Colorado Island, *Croat 7115, 7244, 7346, 7464* (all MO). Cerro Luisa near Pedro Miguel, *Croat 12382* (MO). Barro Colorado Island, *Croat 12949, 13121* (both MO); near Coco Solo Weather Station, *Duke 4283* (MO). Fort Sherman Site, U. S. Army Tropic Test Center, *Dwyer 7173* (MO). Cerro Galera, 350–400 m, *Gentry 6663* (MO). Between Summit and Gamboa, *Greenman & Greenman 5263* (MO). Gamboa, *Kennedy et al. 2327* (MO). Near Gamboa, *Kennedy & Steiner 2457* (MO). Between Frijoles and Monte Lirio, 30 m, *Killip*

12165 (US). Fort San Lorenzo, Fort Sherman Military Reservation, *Maxon & Valentine 7009* (US). Fort San Lorenzo, *McDaniel 5176* (MO). Empire to Mandinga, *Piper 5486* (US). Río Grande, near Culebra, 50–100 m, *Pittier 2138* (US). Near Gatún, *Standley 27294* (US). Balboa, *Standley 29320* (US). Río Pedro Miguel, near East Paraíso, *Standley 30017* (US). Darién Station, *Standley 31607* (US). Quebrada Melgada, 70–75 m, *Steyermark 17472, 17491* (both MO). Old Fort San Lorenzo, *Tyson 1546* (MO). Barro Colorado Island, *Wetmore & Abbe 137* (MO); *Wilson 20* (MO); *Woodworth & Vestal 472* (MO). CHIRIQUÍ: 2 km N of Punta de Burica, 40–80 m, *Busey 763* (MO). Burica Peninsula, 2 mi SW of Puerto Armuelles, 0–200 m, *Croat 22082* (MO). Boquete, Llanos Francia, 4 mi from Boquete toward Dolega, ca. 4500 ft, *Dwyer & Hayden 7586* (MO). 4.1 mi from Boquete on the road to David, *Kirkbride 92A* (MO). Quebrada Melliza, 6 mi S of Puerto Armuelles, 0–150 m, *Liesner 487* (MO). 5 mi S of Boquete toward David, 2800 ft, *McDaniel 6794* (MO). Vic. of San Félix, 0–120 m, *Pittier 5252* (US). Vic. of Puerto Armuelles, 0–75 m, *Woodson & Schery 827* (MO). COCLÉ: Vic. of Natá, 50 m, *Allen 840* (MO). El Valle de Antón, 1000–2000 ft, *Lewis et al. 2542* (MO). Boca del Toabre at confluence of Río Toabre and Río Coclé del Norte, *Lewis et al. 5550* (MO). COLÓN: Near Achiote, *Correa & Dressler 414* (MO, US). East Santa Rita lumber road, *Correa & Dressler 650* (MO). 1 mi N of María Chiquita, *Croat & Porter 11367* (MO). Road to Porto Bello between the Río Piedres and Portobelo, *Elias & Kirkbride 1649* (MO). Portobelo, 0–20 m, *Pittier 2457* (US). DARIÉN: Río Chico from Yaviza at junction with Río Chucunaque to ca. 1 hour by outboard from junction, *Burch et al. 1084* (MO). Vic. of Piñas, *Duke 10615* (MO). Camp Dubaganala helipad, 1371 ft, *Duke 15494* (OS, REED). Camp Summit, Darién–San Blas border along Sea Level Canal, Route 17, 1000–1200 ft, *Oliver et al. 3693* (MO). Along the Sambú River, *Pittier 5545* (US). 3 mi E of Santa Fe, *Tyson et al. 4653* (MO). HERRERA: 4 mi S of Los Pozos, *Tyson 2653* (MO). 10 mi S of Ocú, *Tyson et al. 2825* (MO). LOS SANTOS: Between Tonosí and Macaracas, *Oliver et al. 3572* (MO). PANAMÁ: Isla Taboga, 0–350 m, *Allen 1265* (MO). Road past Cerro Jefe toward La Eneida, *Croat 13071* (MO). Cerro Campana, *Duke 5970* (MO). 10–15 km from Bayano crossing on trail to Santa Fe, *Gentry 3824* (MO). Cerro Jefe, ca. 1000 m, *Gentry 6751* (MO). Between Cañita and dam site, *Gentry & Tyson 1709* (MO). 5 mi SW of Cerro Brewster, ca. 1000 ft, *Lewis et al. 3467* (MO). Road from El Llano to Cartí Tupile, 3 mi above Pan-Am. Hwy., ca. 200 m, *Liesner 707* (MO). Tobago Island, *Standley 27053* (US), *27941* (US). Río Tapia, *Standley 28268* (US). Río Tocumen, *Standley 29484* (US). Tumba Muerto near Panamá, *Standley 29730* (US). Juan Díaz, *Standley 30459* (US). Between Las Sabanas and Matías Hernández, *Standley 31841* (US). Cerro Jefe, 2700 ft, *Tyson 3366* (MO). Coronado Beach, *Tyson 5942* (MO). 6 mi E of Río Pacora, *Tyson 6292* (MO). Road to Cerro Campana, ca. 1000 ft, *Tyson 6419* (MO). SAN BLAS: Vic. of Puerto Obaldía, *Croat 16985* (MO). Opposite Achituppu, *Lewis et al. 94* (MO, US). VERAGUAS: Hills W of Soná, ca. 500 m, *Allen 1027* (MO). Above Santa Fe on slope of Cerro Tuté, 1200–1400 m, *Gentry 6269* (MO). El Embalsadero, 8 mi W of Santiago, *Tyson 6095* (MO).

10. **Mikania pittieri** B. L. Robinson, Proc. Boston Soc. Nat. Hist. 31: 255. 1904. TYPE: Costa Rica, Cuesta de los Borucas, *Pittier 10540* (US).

M. nubigena B. L. Robinson, Contr. Gray Herb. 77: 57. 1926. TYPE: Costa Rica, Las Nubes, San José Prov., *Standley 38509* (US, holotype; GH, isotype).

Sparingly branched herbaceous *vines*; stems greenish to brownish, terete, distinctly striate, often fistulose. *Leaves* opposite; blades ovate, 5–10 cm long and 2.0–4.5 cm wide, the base rounded, the margins entire to subentire, the apex caudate-acuminate, the surface glabrous without glandular punctations, 2 pairs of strongly ascending secondary veins in the basal fifth of the blade, the finer vein reticulations with prominent, included, branched vein endings; petioles slender, 1–2 cm long. *Inflorescence* a panicle with paniculate branches, the branches puberulous; ultimate branches 0–1 mm long. *Heads* 7–8 mm high; subinvolucral bract ovate-lanceolate, 1.5–2.0 mm long, glabrous outside; involucral bracts narrowly oblong with rounded tips, ca. 5 mm long, ca. 1 mm wide, glabrous on the

outer surface except on the somewhat pitted swollen base; corolla whitish, ca. 3 mm long, the tube 1.2–1.5 mm long, the limb narrowly campanulate with short lobes about as long as wide, few glands or hairs outside, usually a few hairs on the tube, the corolla cells quadrate to short-oblong, ca. 25 μ wide; anther appendages firm, rounded, about as long as wide; style base thickened, glabrous, the style appendages with short papillae. *Achenes* 5-ribbed, ca. 4 mm long, glabrous or with numerous small glands; pappus of 35–40 slender bristles in 1 series, tips distinctly enlarged.

Mikania pittieri is known from only Costa Rica and western Panama. The glabrous, caudate-acuminate leaves with the prominent included veinlets are the most distinctive feature of the species.

CHIRIQUÍ: Boquete, Bajo, Chorro, 6000 ft, *Davidson 167* (MO, US).

11. **Mikania psilostachya** DC., Prodr. 5: 190. 1836. TYPE: Peru, *Poeppig 2344* (G-DC, not seen, US, microfiche; B, destroyed, US, photo).

M. scabra DC., Prodr. 5: 190. 1836. TYPE: French Guiana, Cayenne, *Patris* (G-DC, not seen, US, photo).
M. racemulosa Benth., Ann. Nat. Hist. 2: 109. 1839. TYPE: British Guiana, *Schomburgk 480* (US).
M. psilostachya DC. var. *scabra* (DC.) Baker in Mart., Fl. Bras. 6(2): 265. 1876.
M. psilostachya DC. var. *racemulosa* (Benth.) Baker in Mart., Fl. Bras. 6(2): 266. 1876.
M. karuaiensis Badillo, Bol. Soc. Venez. Ci. Nat. 10: 296. 1946. TYPE: Venezuela, Santa Teresita de Kavanayén, Gran Sabana, Bolívar, *Steyermark 59372* (VEN).

Sparingly branched, woody *vines*; stems brownish to slightly reddish, terete to slightly quadrangular, slightly striate, densely short-puberulous, never fistulose. *Leaves* opposite; blades ovate to elliptical, to 15 cm long and 8 cm wide, the base narrowly rounded to shortly cuneate, the margins usually remotely subserrulate, the apex sharply acute to slightly acuminate, the upper surface scabrid, the lower surface distinctly short- usually brownish-puberulous and prominently glandular punctate, 2–3 pairs of strongly ascending secondary veins arising in the basal half of the blade, smaller vein reticulations prominent; petioles ca. 1 cm long, petioles of the largest leaves to 3 cm long. *Inflorescence* a panicle with elongate, strictly spicate or racemose branches, the ultimate branches 0–6 mm long, minutely puberulous. *Heads* 7–9 mm high; subinvolucral bract situated at the base of the pedicel, linear-lanceolate, 1.5–2.0 mm long, densely puberulous abaxially; involucral bracts oblong-lanceolate with short-acute tips, ca. 5 mm long, ca. 1 mm wide, brownish-puberulous and sparsely glandular-punctate outside; corolla white, 4.0–5.0 mm long, the tube narrow, 1.0–1.5 mm long, the limb narrowly campanulate to tubular, cleft ⅕–⅓ of the length into short- or elongate-triangular lobes, few to many glands and hairs on the outer surface, the corolla cells oblong, 15–25 μ wide, often with sinuous walls; anther appendages firm, ovate-triangular, half again as long as wide; style base glabrous, the style appendages usually slightly tapering, with short papillae. *Achenes* 4–5-ribbed, 2.5–3.0 mm long, with many glands and scattered hairs; pappus of ca. 40 slender bristles mostly in 1 series, the tips gradually enlarged.

Mikania psilostachya occurs throughout most of northern South America reaching south to Brazil and Bolivia. The species reaches its northwestern limit in Panama. The presence of pedicels has been used to distinguish *M. scabra* but the character is variable. The Panamanian plants have short corolla limbs and deeply cut lobes that are different from the long-limbed and short-lobed corollas in typical *M. psilostachya* and *M. scabra*. Corollas similar to those in the Panamanian plants occur in some specimens from Brazil. The seemingly similar, deeply lobed corollas in the type specimen of *M. racemulosa* are different in having much longer basal tubes.

CANAL ZONE: Gaillard Hwy. near Gamboa, *Croat 11952* (MO). COLÓN: María Chiquita, E of Río Piedras toward Portobelo, *Dwyer & Kirkbride 7799* (MO). Santa Rita Ridge, 2–3 mi from Transisthmian Hwy., *Gentry 1866* (MO). PANAMÁ: Cerro Azul, *Dwyer 2631, 2794* (both MO). Cerro Jefe, *Dwyer 8511* (MO). Cerro Azul, near Goofy Lake, *Ebinger 980* (MO, US). Cerro Azul, 2000 ft, *Tyson 2072, 2161* (both MO).

12. **Mikania tonduzii** B. L. Robinson, Proc. Boston Soc. Nat. Hist. 31: 256. 1904.
TYPE: Costa Rica, Tucurrique, 635 m, *Tonduz 13274* (GH, not seen).

Coarse herbaceous to somewhat woody, sparingly branched *vines*; stems brownish, terete to slightly hexagonal, striate, minutely puberulous, usually fistulose. *Leaves* opposite; blades broadly ovate, to 15 cm long and 8 cm wide, the base broadly rounded, the margins entire, the apex abruptly narrow-acuminate, sometimes apiculate, the surface slightly puberulous to glabrate with small glandular punctations, 2–3 pairs of prominent secondary veins arching outward and upward from lower fifth of the blade, the tertiary veins regularly transverse; petioles slender, mostly 2–6 cm long. *Inflorescence* a panicle with glomerulate-corymbose secondary and tertiary branches, the branches minutely puberulous, the ultimate branches 0–1 mm long. *Heads* 7–8 mm high; subinvolucral bract linear-lanceolate, minute, 0.3–0.8 mm long, minutely puberulous; involucral bracts short-oblong with rounded tips, ca. 2.0–2.5 mm long including fused swollen bases, ca. 0.8 mm wide, whitish-puberulous and minutely glandular-punctate on the outer surface; corolla white, ca. 4.5 mm long, narrowly funnelform, the tube indistinct, the lobes short, about half again as long as wide with few glands and short hairs on outer surface, the corolla cells quadrate to short-oblong, 20–30 μ wide; anther appendages firm, rather oblong, slightly longer than wide; style base glabrous, the style appendages with short papillae. *Achenes* 5-ribbed, ca. 2 mm long, the sides with scattered, short, often distorted bristles; pappus of 40–50 slender slightly scabrous bristles in 1 series, the apices slightly to distinctly enlarged.

Mikania tonduzii is distributed from southern Mexico south to Panama. The species is rather distinct in the narrow corolla without a well demarcated tube. The closely related *M. globosa* Coult. of Guatemala, Honduras, and Mexico differs by the even more tightly clustered heads and by the broadly truncate involucral bracts with broad scarious margins.

CANAL ZONE: Barro Colorado Island, *Croat 7972* (MO, US).

13. **Mikania tysonii** R. M. King & H. Robinson, Phytologia 28: 275. 1974. TYPE: Panama, top of Cerro Jefe, 3000 ft, *Tyson et al. 4429* (US, holotype; MO, isotype).

M. wedelii Holmes & McDaniel, Phytologia 33: 1. 1976. TYPE: Panama, Bocas del Toro, *von Wedel 2041* (MO).

Slender, decumbent to epiphytic *vines* or *subshrubs*, few to many branched; stems brown, terete to slightly hexagonal, usually glabrous, larger stems narrowly fistulose. *Leaves* opposite; blades elliptical to obovate, to 8 cm long and 3.5 cm wide, the base cuneate, the margins entire, the apex bluntly rounded to short-acuminate, the surface glabrous, usually with reddish glandular punctations, the surface of dried material finely wrinkled and sometimes hiding punctations, 2 pairs of parallel ascending secondary veins from near base; petioles slender, 0.5–1.5 cm long. *Inflorescence* a loose irregular, corymbose panicle, the ultimate branches 1.5–6.0 mm long, sparsely puberulous. *Heads* ca. 5 mm high; subinvolucral bract narrowly oblong, ca. 1.5 mm long, borne 0.5–2.0 mm below most heads; involucral bracts oblong with rounded tips, ca. 3.5 mm long, 1 mm wide, sparsely puberulous and usually with reddish glands outside; corolla white, 4–5 mm long, the tube short, indistinct, with glands on outer surface, the lobes about twice as long as wide; anther appendages firm, broadly oblong-ovate; style base slightly enlarged, glabrous, the style appendages with short papillae. *Achenes* with 4–5 ribs, 2–3 mm long, with many scattered glands, sometimes puberulous; pappus of ca. 50 slender bristles mostly in 1 series, the tips distinctly enlarged.

The species is endemic to Panama where it shows some variation of habit. The plants from central Panama are more shrubby and terrestrial while those from farther west are more scandent and epiphytic. All specimens share the indefinitely corymbose inflorescence, the narrow corollas with indistinct tubes, and the leaves with two pairs of veins from near the base. No close relatives are evident in Panama or the adjacent countries. A similar aspect is found in *Mikania lucida* Blake of Venezuela but that species can be distinguished by its smaller, short, thin anther appendages and usually smooth upper leaf surfaces.

BOCAS DEL TORO: Old Bank Island, vic. of Chiriquí Lagoon, *von Wedel 2041* (MO). COCLÉ: La Mesa, 5 mi N of El Valle, 2500 ft, *Tyson et al. 2445* (US). PANAMÁ: Top Cerro Jefe, 3000 ft, *Tyson et al. 4429* (MO, US). Cerro Jefe, 2900 ft, *Dwyer & Gauger 7378* (MO).

14. **Mikania zonensis** R. M. King & H. Robinson, Phytologia 28: 275. 1974. TYPE: Panama, Albrook, U.S. Army Tropic Test Center Site, Canal Zone, *Dwyer & Robyns 115* (MO, holotype; US, isotype).

Coarse, sparingly branched *vines*; stems becoming dark brownish, terete, striate, glabrate, usually narrowly fistulose. *Leaves* opposite; blades elliptical-ovate, to 21 cm long and 8 cm wide, the base rounded to short-cuneate, the margin entire, the apex narrowly caudate-acuminate, the surface glabrate, 2 pairs of prominent, strongly ascending, secondary veins from near base, the vein reticulation slightly prominent; petioles slender, to 4 cm long. *Inflorescence* rather densely corymbose with almost all heads in clusters of 3, the ultimate branches 0–1 mm long. *Heads* ca. 8–9 mm high; subinvolucral bract minutely

lanceolate, ca. 1 mm long, puberulous distally; involucral bracts oblong with rounded tips, ca. 5 mm long and 1.5 mm wide, the outer surface striate and glandular-punctate, puberulous toward the tip; corolla whitish, ca. 5 mm long, the tubes narrow, ca. 2 mm long, glandular-punctate outside, the limb narrowly funnelform, the lobes short-triangular, about as long as wide with scattered hairs outside, the corolla cells subquadrate to short-oblong, 20–30 μ wide; anther appendages firm, triangular, about twice as long as wide; style base slender, sparsely papillose, the style appendages hirsute with many long papillae. *Achenes* with 5 ribs or grooves, thickly corticated and nearly terete when fully mature, ca. 3.5 mm long; pappus of ca. 60 slender bristles, the tips not or only slightly enlarged.

Mikania zonensis is known only from the type collection in the Panama Canal Zone. The species is close to *M. guaco* but differs in the more elliptical, less decurrent, more coriaceous, and more glabrous leaf blades.

CANAL ZONE: Albrook Field: U. S. Army Tropic Test Center Site, *Dwyer & Robyns 115* (MO, US).

28. NEOMIRANDEA

Neomirandea R. M. King & H. Robinson, Phytologia 19: 306. 1970. TYPE: *Eupatorium araliaefolium* Less.

Small *shrubs* to small *trees* with few to many branches, growing in deep humus or epiphytic; stems and leaves usually somewhat fleshy. *Leaves* opposite or in whorls of 3, short- to long-petiolate; blades narrowly elliptical to orbicular, the bases cuneate to cordate, the margins entire to coarsely lobed and dentate. *Inflorescence* broadly corymbose-paniculate. *Heads* with 2–28 florets; involucre of ca. 9–15 subimbricate to imbricate bracts, in 3–4 series, the outer bracts spreading at maturity, the inner bracts deciduous; receptacle flat to slightly convex, glabrous or sometimes short-puberulous; corolla tubular to narrowly funnelform with usually indistinct narrow tube, the lobes smooth, usually short (deeply cleft in four species), the outer surface with hairs or glands, the inner surface glabrous or with many hairs, the cells of the corolla usually subquadrate with straight walls, rarely with slightly sinuous walls; anther collar elongate with many quadrate or short-oblong cells in lower part, the cell walls without ornate thickenings, the exothecial cells mostly subquadrate or broader than long, the anther appendage ovate or oblong, longer than broad; style base glabrous, with or without prominent enlargement, the style appendages linear, smooth, scarcely broadened above, the tip rounded. *Achenes* prismatic with 5 ribs, glabrous or with few to many bristles; carpopodium short with subquadrate rather thin-walled cells in few to many series; pappus of 30–57 scarcely scabrous bristles, the apical cells shortly to sharply acute. *Pollen* with short spines.

Neomirandea is a genus of approximately 24 species ranging from Mexico through Central America to Colombia and Ecuador in South America. The greatest number of species is found in the area of Costa Rica and western Panama. The genus is divided into two basic groups. The typical subgenus is characterized by an enlarged style base, the carpopodium with small cells in many series, and the

corolla often with hairs on the inner surface. The subgenus *Critoniopsis* is characterized by style bases not enlarged, the carpopodium with larger cells in few series, and the corolla always glabrous inside. Eleven species have been collected in Panama.

Literature:

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——— & ———. 1975a. Studies in the Eupatorieae (Asteraceae). CXXXVI. Four new species of *Neomirandea*. Phytologia 29: 351–361.

——— & ———. 1975b. Studies in the Eupatorieae (Asteraceae). CXXXVII. Two new species of *Neomirandea*. Phytologia 30: 9–14.

a. Leaf margins lobed or serrate, blades broadly ovate to deltoid or aceriform.
  b. Leaf blades strongly dentate to lobed; corolla without internal hairs .... 9. *N. panamensis*
  bb. Leaf blades ovate or broadly ovate, the margins serrate; corolla with internal hairs.
    c. Involucral bracts ovate; heads with mostly 15–20 florets; corolla tube half as long as the limb ---------- 8. *N. homogama*
    cc. Involucral bracts oblong to elliptical; heads with mostly 5–12 florets; corolla tube usually shorter than limb ---------- 11. *N. standleyi*
aa. Leaf margins entire to remotely serrulate, blades ovate to oblong.
  d. Corolla with hairs inside; style node enlarged; florets white.
    e. Heads with 18–28 florets; corolla with lobes less than half again as long as wide ---------- 2. *N. araliaefolia*
    ee. Heads with ca. 5 florets; corolla deeply cleft, lobes twice as long as wide ---------- 10. *N. pseudopsoralea*
  dd. Corolla without hairs inside; style node not enlarged; florets lavender or purple.
    f. Outer involucral bracts orbicular, inner bracts prominently striate ------- 3. *N. arthodes*
    ff. Outer involucral bracts narrow, inner bracts not striate.
      g. Heads with 5 florets ---------- 5. *N. croatii*
      gg. Heads with 8–10 florets.
        h. Leaves subsessile, the petioles 1–5 mm long; corolla with hairs or glands on outer surface.
          i. Leaf blades with remotely serrulate margins, the lower surface sparsely puberulous; petioles narrow ---------- 7. *N. gracilis*
          ii. Leaf blades with entire margins, the lower surface without hairs; petioles greatly thickened ---------- 1. *N. allenii*
        hh. Leaves distinctly petiolate, the petioles 5–12 mm long; corolla glabrous.
          j. Leaf tips blunt, rounded; corolla narrowly tubular with lobes ca. 1½ times as long as wide ---------- 4. *N. chiriquensis*
          jj. Leaf tips sharply acuminate; corolla funnelform with lobes about as long as wide ---------- 6. *N. eximia*

1. **Neomirandea allenii** R. M. King & H. Robinson, Rhodora 74: 273. 1972. TYPE: Panama, region of El Valle de Antón, Coclé, *Allen 3643* (NY, holotype; F, MO, P, isotypes).

Epiphytic *shrubs* to 1.5 m tall; stems terete, minutely puberulous. *Leaves* opposite, subsessile; blades fleshy, broadly elliptical to obovate, to 9 cm long and

6 cm wide, the base short-cuneate to slightly rounded, the margins entire, rarely slightly serrulate, the apex obtusely acute to narrowly rounded, the surfaces with glandular punctations and without hairs, the venation pinnate, the secondary veins prominent; petioles ca. 3–5 mm long, greatly thickened, glabrous. *Inflorescence* a corymbose panicle, to 10 cm wide and 10 cm high; ultimate branches ca. 5 mm long, puberulous. *Heads* 8–9 mm high with ca. 10 florets; involucral bracts ca. 12, subimbricate, in 2–3 series, broadly lanceolate, mostly 2–3 mm long and 0.5 mm wide, the outer surface sparsely puberulous and with glandular punctations; receptacle glabrous; corolla pink or purple, ca. 5 mm long, narrowly funnelform without hairs inside, the lobes about as long as wide with numerous glands on outer surface, the glands mostly long-stalked; style base not enlarged. *Achenes* prismatic, with few long-stalked glands and uniseriate multiseptate hairs, the glands and hairs more numerous at base and apex; carpopodium with larger cells in a few series; pappus of ca. 30 scabrous bristles, mostly ca. 5 mm long, the apical cells of some bristles acute, few to many interspersed bristles with enlarged tips and blunt apical cells.

Neomirandea allenii is known from Panama and northern Colombia. The species is the most commonly collected member of the genus in Panama, being common at lower and medium elevations in the central part of the country. The species can usually be distinguished by the broad, nearly sessile leaves with thick petioles and by the many pappus setae with blunt, thickened apices.

COCLÉ: Region of El Valle de Antón, 1000 m, *Allen 3643* (F, MO, NY, P). Between Cerro Pilón and El Valle de Antón, 700–900 m, *Duke & Dwyer 13979* (MO). El Valle de Antón, ca. 2000 ft, *Dwyer & Correa 7990* (MO). Cerro Pilón, 3100 ft, *Dwyer & Lallathin 8973* (MO). 8 mi N of El Valle de Antón, *Luteyn & Kennedy 1671* (MO). DARIÉN: Headwaters of Río Tuquesa, ca. 350 m, *Croat 27224* (MO, US). PANAMÁ: Cerro Jefe, ca. 2900 ft, *Dwyer & Gauger 7384* (MO). Near Cerro Campana, *Kirkbride & Hayden 336* (MO). Cerro Jefe, 3000 ft, *Tyson et al. 4427, 4447* (both MO). VERAGUAS: Río Primero Brazo, 25 km beyond Agriculture School, *Croat 25519* (MO, US). Río Dos Bocas, 12 km beyond Santa Fe, *Croat 25886* (MO, US). 5–8 km beyond Escuela Agrícola Alto Piedra, 730–770 m, *Croat 25925* (MO).

2. **Neomirandea araliaefolia** (Less.) R. M. King & H. Robinson, Phytologia 19: 307. 1970.—FIG. 29.

Eupatorium araliaefolium Less., Linnaea 6: 402. 1831. TYPE: Mexico, sylvae Misantlae, *Schiede & Deppe 1242* (B, destroyed; MO, isotype, US, photo).

E. omphaliaefolium Kunth & Bouché, Ind. Sem. Hort. Berol. adnot. no. 13. 1844; ex Walp., Repert. Bot. 6: 113. 1846. TYPE: Mexico (B, destroyed).

E. heterolepis B. L. Robinson, Proc. Amer. Acad. Arts 35: 335. 1900. TYPE: Guatemala, E portions of Vera Paz and Chiquimula, 1885, *Watson 65* (US, isotype).

E. altiscandens McVaugh, Contr. Univ. Michigan Herb. 9: 390. 1972. TYPE: Mexico, 21–24 km S of El Chante (ca. 25 km SE of Autlán), Jalisco, *McVaugh 23092* (MICH, holotype; US, isotype).

Epiphytic *shrubs* to 4 m tall; stems terete, with faint striations, glabrous. *Leaves* opposite; blades slightly fleshy, ovate to elliptical, to 16 cm long and 7 cm wide, the base broadly cuneate, the margins entire, the apex sharply acute, the surfaces glabrous, the venation pinnate, the secondary veins prominent; petioles to 6 cm long, glabrous. *Inflorescence* a corymbose panicle, to 12 cm wide and 12 cm high, the ultimate branches ca. 5 mm long, densely puberulous. *Heads* ca. 1

cm high, with ca. 18–28 florets; involucral bracts ca. 25–28, unequal, imbricate, in 3–4 series, the outer series ovate to narrowly oblong, mostly 2–4 mm long, scarcely puberulous, the inner series to 7 mm long, lanceolate with often irregularly laciniate margins, glabrous; receptacle minutely puberulous; corolla white, ca. 5 mm long, narrowly funnelform with hairs on inner surface, few hairs on outer surface, the lobes less than half again as long as wide; style base enlarged, glabrous. *Achenes* prismatic, densely puberulous; carpopodium distinct, the cells small in many series; pappus of ca. 30–35 scabrous bristles, mostly ca. 5.5 mm long, the apical cells acute.

Neomirandea araliaefolia is widely distributed from Veracruz and Jalisco in Mexico southward to Panama. The species was the first member of the genus to be collected and described. The species seems to occur in two slightly different forms. The typical form is most common at lower elevations and has a more acute leaf base and scarcely lacinate inner involucral bracts. Specimens from Guatemala, Mt. Ovando in Chiapas, and from Panama have more abrupt leaf bases and laciniate inner involucral bracts.

CHIRIQUÍ: Vic. of "New Switzerland," central valley of Río Chiriquí Viejo, 1800–2000 m, *Allen 1361* (F, MO, US).

3. **Neomirandea arthodes** (B. L. Robinson) R. M. King & H. Robinson, Phytologia 19: 308. 1970.

Eupatorium arthodes B. L. Robinson, Contr. Gray Herb. 68: 8. 1923. TYPE: Costa Rica, La Palma 1550 m, *Tonduz 12430* (US).

Epiphytic *shrubs* to 3 m tall; stems terete, scarcely striate, glabrous, narrowly fistulose. *Leaves* opposite; blades fleshy, broadly elliptical, to 12 cm long and 5 cm wide, the base cuneate, the margins entire, the apex sharply acuminate, the surfaces glabrous, the venation pinnate, the secondary veins somewhat prominent; petioles to 3.5 cm long, glabrous. *Inflorescence* a corymbose panicle, to 25 cm wide and 10 cm high, the ultimate branches ca. 5 mm long, scarcely puberulous. *Heads* ca. 1 cm high, with ca. 12 florets; involucral bracts ca. 20, imbricate, in ca. 4 series, strongly unequal, 1–7 mm long, the outer surface glabrous, mostly prominently striate, the outer bracts orbicular to broadly oblong, the inner bracts narrowly oblong, the apices rounded; receptacle sparsely minutely puberulous; corolla pink or lavender, ca. 6 mm long, narrowly funnelform, without internal hairs, glabrous on outer surface, the lobes ca. twice as long as wide; style base not enlarged, glabrous. *Achenes* prismatic with narrow bases, ca. 2.8 mm long, minutely scabrid on base and ribs; carpopodium distinct, with lax cells in 4–5 rows; pappus of ca. 35–40 scabrous bristles, ca. 5 mm long, the apical cells subacute.

Neomirandea arthodes is known from Costa Rica and western Panama. The species is the only member of the subgenus *Critoniopsis* in Panama with broad outer involucral bracts.

BOCAS DEL TORO: Robalo Trail, N slopes of Cerro Horqueta, 6000–7000 ft, *Allen 4927* (MO). CHIRIQUÍ: Vic. of Bajo Chorro, 1900 m, *Woodson & Schery 606* (MO).

FIGURE 29. *Neomirandea araliaefolia* (Less.) R. M. King & H. Robinson.—A. Habit (× 2/5).—B. Head (× 5½).—C. Achene (× 6⁹/₁₀).—D. Corolla (× 6⁹/₁₀).—E. Style (× 6⁹/₁₀).

4. **Neomirandea chiriquensis** R. M. King & H. Robinson, Phytologia 27: 245. 1973. TYPE: Panama, Boquete, Chiriquí, *Stern et al. 1086* (MO).

Shrubs to 1.5 m tall; stems terete, glabrous. *Leaves* opposite; blades fleshy to coriaceous, broadly elliptical to obovate, 6–11 cm long and 2.5–6.5 cm wide, the base cuneate, the margins entire, the apex rounded to subacute, the surface with sparse glandular punctations, otherwise glabrous, the secondary veins obscure, strongly ascending; petioles rather slender, to 1 cm long, glabrous. *Inflorescence* a corymbose panicle, to 20 cm wide and 10 cm high, the ultimate branches 5–10 mm long, densely minutely puberulous. *Heads* ca. 7 mm high and ca. 3 mm wide with 8–10 florets; involucral bracts violet, ca. 15, subimbricate, in ca. 3 series, lanceolate to linear, 1.5–5.0 mm long and 0.7–1.0 mm wide, the apex with slight fringe, the outer surface glabrate; receptacle glabrous or minutely spiculiferous; corolla white at anthesis and becoming red-violet, ca. 4 mm long, narrowly funnelform, glabrous inside and outside, the lobes ca. half again as long as wide; style base not enlarged, glabrous. *Achenes* prismatic with narrow bases, ca. 2.5 mm long, mostly glabrous, a few spicules at upper end; carpopodium distinct, the cells in 3–5 series; pappus of ca. 40 scabrous bristles, mostly ca. 3.5 mm long, the apices of many bristles somewhat enlarged, the apical cells subacute.

Neomirandea chiriquensis is known only from the type collection. In appearance the species seems rather like a *Clusia*. Closest relationship is probably to *N. allenii* which has somewhat similar leaf blades and similar enlarged tips on the pappus setae. The species differs in many details including the distinctly petiolate leaves, the longer more glabrous involucral bracts, and the totally glabrous corollas. The single specimen indicates a distribution to the west of that of *N. allenii* and at higher elevations.

CHIRIQUÍ: Boquete, Palo Alto, 5000 ft, *Stern et al. 1086* (MO).

5. **Neomirandea croatii** R. M. King & H. Robinson, Phytologia 29: 352. 1975. TYPE: Panama, Las Nubes near Cerro Punta, Chiriquí, *Croat 26452* (US).

Epiphytic slightly fleshy *shrubs* to 1 m high; stems terete, densely hirsute. *Leaves* opposite; blades slightly fleshy to coriaceous, broadly elliptical to slightly obovate, mostly 5.5–9.5 cm long and 3.0–6.5 cm wide, the base cuneate, the margins entire, the apex slightly short-acuminate, the upper surface sparsely hispidulous, the lower surface sparsely pilose, more densely pilose on primary vein, the secondary veins pinnate, prominent; petioles narrow, mostly 5–10 mm long. *Inflorescence* a broadly corymbose panicle, to 15 cm wide and 12 cm high, the branches puberulous, the ultimate branches 2–9 mm long. *Heads* ca. 9 mm high and 1.5–2.0 mm wide, mostly with 5 florets; involucral bracts 8–9, subimbricate, in ca. 3 series, linear-lanceolate with narrowly obtuse tips, 3–6 mm long and 0.8–1.0 mm wide, the outer surface minutely puberulous and very sparsely glanduliferous; receptacle flat, minutely puberulous; corolla lavender or purplish, ca. 7 mm long, narrowly funnelform, the inner surface glabrous, the tube and lower limb mostly glabrous on outer surface, the lobes ovate-oblong, ca. 0.8 mm long and 0.5–0.6 mm wide, with outer surface sparsely glanduliferous and minutely puberulous; style base not enlarged. *Achenes* prismatic, 2.5–3.0 mm

long, mostly glabrous, puberulous with short bristles near upper and lower ends; carpopodium a distinct rim; pappus of ca. 50 slightly scabrous bristles, with slightly enlarged tips, the apical cells acute.

Neomirandea croatii is known only from the type collection. The species has a superficial resemblance to *N. chiriquensis* from the same general region, but the latter is a glabrous species with more florets per head and with more obscure, more ascending secondary veins in the leaf.

CHIRIQUÍ: Las Nubes near Cerro Punta, ca. 2000 m, *Croat 26452* (US).

6. **Neomirandea eximia** (B. L. Robinson) R. M. King & H. Robinson, Phytologia 19: 309. 1970.

Eupatorium eximium B. L. Robinson, Contr. Gray Herb. 73: 11, 1924. TYPE: Costa Rica, vic. of La Palma on road to La Hondura, 1500–1700 m, *Maxon & Harvey 7941* (US).

Small epiphytic *shrubs* 1–2 m tall; stems terete, faintly striate, glabrous. *Leaves* opposite; blades fleshy, elliptical, to 8 cm long and 3 cm wide, the base cuneate, the margins usually entire, the apex sharply acuminate, the surfaces glabrous, without evident glandular punctations, the lower surface somewhat paler, the primary vein distinct, the secondary veins usually totally obscure, strongly ascending; petioles to 1.2 cm long, glabrous. *Inflorescence* a loose corymbose panicle, to 12 cm high and 15 cm wide, the ultimate branches ca. 9–14 mm long, densely puberulous. *Heads* ca. 1 cm high with ca. 9 florets; involucral bracts purple-tinged, ca. 15, subimbricate, in ca. 3 series, 1.5–5.0 mm long, broadly lanceolate with narrowly rounded to subacute tips, the outer surface glabrate; receptacle glabrous; corolla lavender, ca. 4 mm long, narrowly funnelform, glabrous or with a few minute hairs on lobes, the lobes as long as wide to somewhat longer; style base not enlarged, glabrous. *Achenes* prismatic, 2.5–3.0 mm long, glabrous or with a few bristles; carpopodium a narrow rim, the cells in 3–5 series; pappus of ca. 40 slender, slightly scabrous bristles, ca. 4.5 mm long, the apical cells acute.

Neomirandea eximia is known only from Costa Rica and Panama. The species is common in parts of Costa Rica but seems comparatively rare and variable in Panama. Some Panamanian plants have a few bristles on the achene unlike populations in Costa Rica, and specimens from farthest east tend to have sparser inflorescences and more reduced, slightly serrulate juvenile or secondary leaves. The latter plants may indicate some introgression with the related *N. gracilis* of central Panama.

CHIRIQUÍ: Chiriquí Trail between Quebrada Hondo and Divide, *Kirkbride & Duke 937* (MO, REED). NW side of Cerro Punta beyond Las Nubes, ca. 7500 ft, *Wilbur et al. 13203* (F). VERAGUAS: Mts. 3.5–4.5 mi above Santa Fe, *Gentry 3076* (MO). 5 mi W of Santa Fe on road past Escuela Agrícola Alto Piedra, 800–1200 m, *Liesner 935* (MO, PMA).

7. **Neomirandea gracilis** R. M. King & H. Robinson, Phytologia 29: 353. 1975. TYPE: Panama, Valley of Río Bocas, Veraguas, *Croat 27701* (US).

Small epiphytic *shrubs* to 1 m tall; stems terete, puberulous, becoming glabrous below. *Leaves* opposite; blades papyraceous, oblong-elliptical, mostly 4–8 cm

long and 1.5–3.0 cm wide, the base short-cuneate, the margins distinctly remote-serrulate, the apex shortly acute, the upper surface sparsely punctate, the lower surface sparsely puberulous and densely glandular-punctate, the primary vein subpilose below, the secondary veins pinnate, not very prominent; petioles short, 1–2 mm long. *Inflorescence* a small corymbose panicle, 4.5 cm wide and 3.5 cm high, the branches puberulous and sparsely glanduliferous, the ultimate branches 1.5–6.0 mm long. *Heads* ca. 6 mm high and 1.5 mm wide with 8–9 florets; involucral bracts brown, ca. 12, subimbricate to eximbricate, in ca. 2 series, narrowly oblong with narrowly rounded tips, 1.5–2.5 mm long and ca. 0.4 mm wide, the outer surface sparsely puberulous and glanduliferous; receptacle glabrous; corolla lavender, ca. 4 mm long, narrowly funnelform, the inner surface glabrous, the outer surface puberulous and glanduliferous, the lobes very short-triangular; style base not enlarged. *Achenes* prismatic, ca. 1.7 mm long, puberulous and glanduliferous; carpopodium a distinct rim, the cells in 3–5 rows; pappus of ca. 32–35 slightly scabrous bristles with slightly enlarged tips, the apical cells acute.

Neomirandea gracilis is known only from the type collection. The species is related to *N. eximia* and occurs at the extreme eastern edge of the range of the latter. *Neomirandea gracilis* differs from *N. eximia* by the serrulate and nearly sessile oblong leaves, by the more sparing inflorescence, and by the numerous glands on the corolla lobes. Some material of *N. eximia* from Panama shows similar small inflorescences and some serrulation of the leaf margin which suggests introgression. A few specimens of *N. allenii* also show such tendencies and may indicate some past hybridization.

VERAGUAS: Valley of Río Dos Bocas, between Escuela Agrícola Alto Piedra and Calovébora, 15.6 kms NW of Santa Fe, 450–550 m, *Croat 27701* (US).

8. **Neomirandea homogama** (Hieron.) H. Robinson & R. D. Brettell, Phytologia 28: 62. 1974.

Liabum homogamum Hieron., Bot. Jahrb. Syst. 28: 626. 1901. TYPE: Colombia, near La Conga, region Popayán, *Lehmann 5972* (F, photo and fragment, US).
Eupatorium hitchcockii B. L. Robinson, Contr. Gray Herb. 73: 14. 1924. TYPE: Ecuador, valley of Pastaza River between Baños and Cashurco, Tungurahua, *Hitchcock 21876* (US).
Neomirandea hitchcockii (B. L. Robinson) R. M. King & H. Robinson, Phytologia 19: 308. 1970.

Coarse *herbs* or *shrubs* to 5 m tall, sometimes epiphytic; stems terete or grooved, subglabrous, fistulose. *Leaves* opposite; blades papyraceous to slightly fleshy, ovate to oblong-ovate, to 30 cm long and 20 cm wide, the base cuneate to truncate, the margins serrate to slightly dentate, the apex sharply acute to slightly short-acuminate, the surface glabrate, the venation pinnate with many pairs of secondaries often concentrated in basal fourth; petioles 4–6 cm long, glabrate to sparsely puberulous. *Inflorescence* a loose corymbose panicle, to 20 cm wide and 20 cm high, the ultimate branches 3–12 mm long, densely puberulous. *Heads* 9–11 mm high with 14–21 florets; involucral bracts ca. 20–25, imbricate, in 3–4 series, mostly 2–6 mm long, the apices obtusely acute to narrowly rounded, the outer surface minutely puberulous to glabrate, the outer bracts broadly ovate to sub-orbicular, the inner bracts broadly oblong to oblong-lanceolate; receptacle puberulous; corolla lavender to purple, 5–7 mm long, funnelform with narrow tube

as long as or longer than limb, with numerous hairs on inner surface, few hairs on outer surface, the lobes 0.8–0.9 mm long and 0.6 mm wide, with few nearly sessile glands and few short hairs on outer surface; style base enlarged, glabrous. *Achenes* prismatic, 3–4 mm long, glabrous; carpopodium distinct, with small cells in 8–10 series; pappus of ca. 40 slightly scabrous bristles, mostly 5–7 mm long, the apical cells acute.

Neomirandea homogama is known from Panama southward through Colombia to southern Ecuador. The species is one of a pair that have previously been distinguished primarily by geography and number of florets per head. The presence of both species in Panama and the greater variation in number of florets have resulted in some problems in delimiting the species, and the name *N. homogama* was at one point applied to the related *N. standleyi*. The two species are now recognized as very close relatives with nearly continuous if not slightly overlapping ranges. The more eastern *N. homogama* has larger heads with more prominent, often broadly ovate, outer involucral bracts and 14–21 florets per head. The corollas are generally narrower with tubes usually as long as the limb. The more western *N. standleyi* has smaller heads with usually oblong or elliptical outer involucral bracts that do not project as strongly on their basal margins. There are 5–12 florets per head and the corollas are more generally flaring with tubes distinctly shorter than the limbs. The distribution of characters suggests that two thoroughly distinct species exist with possibly some complications through hybridization.

BOCAS DEL TORO: Chiriquí trail between Quebrada Higueron and Gutierrez, *Kirkbride & Duke 750* (MO, REED, US). COCLÉ: La Mesa above El Valle, *Croat 14304* (MO).

9. **Neomirandea panamensis** R. M. King & H. Robinson, Phytologia 27: 247. 1973. TYPE: Panama, Cerro Horqueta, Bocas del Toro, *Allen 4954* (MO, holotype; US, isotype).

Coarse arborescent perennial *herbs* to 13 m tall; stems with short internodes, strongly striate, densely granulose-puberulous on younger parts. *Leaves* opposite; blades papyraceous, deltoid to aceriform, to 20 cm long and 20 cm broad, the base truncate to distinctly cordate, the margins with large angular lobes, serrate, the apices sharply short-acuminate, the upper surface sparsely puberulous mostly on veins, the lower surface densely puberulous on veins and veinlets, the venation strongly trinervate from at or near base; petioles to 15 cm long, in uppermost leaves sometimes with strongly toothed wing. *Inflorescence* a broad corymbose panicle, to 27 cm wide and 18 cm high, the ultimate branches to 1 mm long, densely granulose-puberulous. *Heads* ca. 6 mm high with 5 florets; involucral bracts ca. 15, imbricate, in 4–5 series, strongly unequal, broadly ovate to oblong, the tips rounded, the outer surface slightly puberulous; receptacle glabrous, corolla lavender, 3.5–4.0 mm long, narrowly funnelform, without hairs on inner surface, with glands on outer surface of tube and lobes, the lobes oblong-lanceolate, ca. 1 mm long and 0.3 mm wide; style base enlarged, glabrous. *Achenes* prismatic with short bristles on upper part; carpopodium short, the cells small, in ca. 8 series; pappus of ca. 45–55 slightly scabrous bristles, mostly 3.5–4.0 mm long, the apical cells acute.

Neomirandea panamensis is known only from the type collection. The species is distinct from all other Panamanian species of the genus by its aceriform leaves. The closest relatives seem to be two Costa Rican species that have similar leaves with variously winged petioles and have the combination of enlarged style bases and glabrous inner surfaces of the corollas. Of these latter species, *N. grosvenorii* R. M. King & H. Robinson differs by the consistently winged petioles, by the greater size of the heads and florets, and by the glabrous corolla tubes. The internodes of the stems also are much longer in the material seen. The other species, *N. burgeri* R. M. King & H. Robinson, has marked retrorsely toothed petiolar wings and a prominent horizontal rootstock. Less closely related is the common *N. angularis* (B. L. Robinson) R. M. King & H. Robinson of Costa Rica which has unwinged petioles, more pubescent lower leaf surfaces, and hairs inside the corolla.

BOCAS DEL TORO: Robalo Trail, N slopes of Cerro Horqueta. 6000–7000 ft, *Allen 4954* (MO, US).

10. **Neomirandea pseudopsoralea** R. M. King & H. Robinson, Phytologia 30: 9. 1975. TYPE: Panama, road between Cerro Punta and Quebrada Iglesia, Chiriquí, *Croat & Porter 16056* (MO, holotype; US, isotype).

Large epiphytic slightly fleshy *shrubs* to 12 m tall with rhizomes reaching the ground; stems terete, slightly striate, sparsely puberulous to glabrous. *Leaves* opposite; blades fleshy, broadly elliptical to slightly ovate, to 12 cm long and 6 cm wide, the base usually short-cuneate, the margins usually entire, the apex distinctly short-acuminate, the surface glabrous, the venation pinnate, the secondary veins not very prominent; petioles 1–5 cm long, glabrous. *Inflorescence* a pyramidal panicle, to 17 cm high and 13 cm wide, the ultimate branches mostly 1–3 mm long, densely puberulous. *Heads* 5–6 mm high with 4–5 florets; involucral bracts ca. 20–25, imbricate, in 4–5 series, strongly unequal, 0.5–4.5 mm long, mostly narrowly ovate to narrowly oblong, the outer surface essentially glabrous, the inner bracts usually deeply cleft at the tip; receptacle sparsely puberulous; corolla white, ca. 3.5 mm long, broadly funnelform, the limb densely hirsute inside, the tube and limb sparsely puberulous outside, the lobes 1.0–1.5 mm long and 0.3–0.4 mm wide, glabrous on outer surface; style base enlarged, glabrous. *Achenes* prismatic, glabrous to slightly scabrid on ribs; carpopodium short, the cells small, in 6–8 series; pappus of 35–40 slightly scabrous bristles, ca. 4–5 mm long, the tips distinctly thickened, the apical cells usually blunt.

Neomirandea pseudopsoralea is known only from western Panama. The species is related to *N. psoralea* (B. L. Robinson) R. M. King & H. Robinson of Costa Rica which has a similar habit. The Costa Rican species differs by the rose-colored corolla with broader lobes and by the inner involucral bracts lacking lacerate tips. The Panamanian species is more closely related to two other Costa Rican species, *N. biflora* R. M. King & H. Robinson and *N. turrialbae* R. M. King & H. Robinson which both differ by their longer heads and corollas and by their reduced number of florets per head.

CHIRIQUÍ: Road between Cerro Punta and Quebrada Iglesia, *Croat & Porter 16056* (MO). E of Guadeloupe, along the Río Chiriquí Viejo ca. 2 mi NE of Cerro Punta, ca. 6500 ft, *Wilbur et al. 13083* (MO). Vic. of Bajo Chorro, 1900 m, *Woodson & Schery 626* (MO).

11. **Neomirandea standleyi** (B. L. Robinson) R. M. King & H. Robinson, Phytologia 19: 308. 1970.

Eupatorium standleyi B. L. Robinson, Contr. Gray Herb. 77: 40. 1926. TYPE: Costa Rica, Alto de La Estrella, Cartago, *Standley 39288* (US).
E. brenesii Standley, Publ. Field Mus. Nat. Hist., Bot. Ser. 18: 1461. 1938. TYPE: Costa Rica, Alto de La Palma de San Ramón, *Brenes 3842* (F, photo US).

Coarse *herbs* or *shrubs* to 3 m tall, sometimes epiphytic; stems terete or somewhat grooved, essentially glabrous, fistulose. *Leaves* opposite; blades papyraceous to slightly fleshy, ovate to oblong-ovate, to 15 cm long and 12 cm wide, the base cuneate to truncate, the margins slightly to coarsely serrate, the apex sharply acute to narrowly short-acuminate, the upper surface essentially glabrous, the lower surface sparsely minutely puberulous, the venation pinnate with many pairs of secondary veins often concentrated in basal fourth; petioles to 7 cm long, glabrous to slightly puberulous. *Inflorescence* a loose sometimes elongate panicle with corymbose branches, to 30 cm wide and sometimes 40 cm high, the ultimate branches mostly 2–5 mm long, rather densely puberulous. *Heads* ca. 7 mm high with 5–12 florets; involucral bracts ca. 18–20, imbricate, in ca. 3 series, unequal, mostly 2–5 mm long, the apices obtusely acute to narrowly rounded, the outer surfaces minutely puberulous to glabrate, the outer bracts narrowly ovate or oblong to elliptical, the inner bracts oblong-lanceolate to lanceolate; receptacle slightly puberulous; corolla lavender, 4.5–5.0 mm long, funnelform, the tube usually 1.5–2.0 mm long, the limb with numerous hairs on inner surface, the lobes 0.7–0.8 mm long and ca. 0.7 mm wide, with few short hairs and few short-stalked glands on outer surface; style base enlarged, glabrous. *Achenes* prismatic, ca. 2 mm long, mostly glabrous with a few spicules at upper end; carpopodium short, the cells small, in ca. 6 series; pappus of 35–50 bristles, the tips not or scarcely enlarged, the apical cells acute.

Neomirandea standleyi is known only from Costa Rica and western Panama. The species is closely related to *N. homogama* and the distinctions are discussed under that species. The Panamanian material of the two species is easily distinguished on the basis of the involucre, but some specimens of *N. standleyi* from Costa Rica have more ovate outer bracts. In Costa Rica there is also the related species, *N. guevarii* R. M. King & H. Robinson, which has much larger involucral bracts than either *N. standleyi* or *N. homogama*.

CHIRIQUÍ: Bajo Mono, Robalo Trail, W slopes of Cerro Horqueta, 5000–7000 ft, *Allen 4821* (MO). Bajo Chorro, Boquete, 6000 ft, *Davidson 318* (F, MO). Río Chiriquí Viejo Valley, between El Volcán and Cerro Punta, *White 17* (MO, US).

29. PIQUERIA

Piqueria Cav., Icon. Descr. Pl. 3: 18. 1794. TYPE: *P. trinervia* Cav.

Erect sparsely branching perennial *herbs*. *Leaves* mostly opposite, usually short-petiolate to sessile; blades ovate to lanceolate with serrate to serrulate

margins, the veins trinervate from base. *Inflorescence* laxly to densely subcymose. *Heads* discoid with 3–5 involucral bracts and florets in equal numbers; involucral bracts equal, in 1 series, spreading when mature; receptacle flat, glabrous; corollas campanulate with a short densely-haired tube, the lobes 5, papillose on inner surface, smaller papillae on outer surface near tip; anther filaments with short to long papillae on lower part, the anther collars broad with cell walls densely covered with annulate thickenings, the exothecial cells subquadrate to broader than long, the anther appendage vestigial or lacking; style base not enlarged, glabrous, the style appendages distinctly enlarged at apex, densely long-papillose below. *Achenes* 5-ribbed with distinctly narrowed base, the lateral surfaces with unusually sparse, minute internal punctations; carpopodium straight or contorted; pappus lacking. *Pollen* with prominent broad spines.

Piqueria contains seven species distributed from Mexico to Central America and the West Indies. One species has been collected in Panama.

Literature:

Robinson, B. L. 1906. Studies in the Eupatorieae. Revision of the genus *Piqueria*. Proc. Amer. Acad. Arts 42: 3–16.

1. **Piqueria trinervia** Cav., Icon. Descr. Pl. 3: 19. 1795. TYPE: Mexico, *Gomez Ortega*? (MA, not seen).—FIG. 30.

P. ovata D. Don in Loud., Hort. Brit. 337. 1830. TYPE: Mexico (LINN?, not seen).
Ageratum febrifugum Ses. ex DC., Prodr. 5: 104. 1836. nom. nud. pro syn.
Stevia febrifuga Moc. ex DC., Prodr. 5: 104. 1836. nom. nud. pro syn.
Piqueria trinervia Cav. var. *luxurians* Kuntze, Rev. Gen. Pl. 1: 355. 1891. TYPE: Costa Rica, Irazú, 3000 m, *Kuntze* (NY?, not seen).
P. luxurians (Kuntze) B. L. Robinson ex Volkens, Verh. Bot. Vereins Prov. Brandenburg 65: 118. 1923.

Erect short-lived perennial *herbs* to 1.5 m high, with few or no branches; stems often pale, terete to slightly quadrangular, puberulous on internodes along opposite surfaces above leaf axils and on upper surfaces of branches, glabrescent. *Leaves* opposite; blades ovate to broadly lanceolate, to 8 cm long and 3.5 cm wide, the base rounded and trinervate, the margins with many coarse serrations, the apex acute to slightly acuminate, the surface glabrous or sparsely puberulous mostly on veins; petioles short but distinct, 2–10 mm long. *Inflorescence* a lax to rather dense panicle with cymose to subcymose branches, the ultimate branches 1–4 mm long, partly puberulous. *Heads* 3.5–4.0 mm high with 3–4 florets and 3–4 involucral bracts, the florets fragrant; involucral bracts eximbricate in 1 series, broadly oblong-elliptical with truncate to emarginate tip and distinctly excurrent mucronate midvein, the margins scarious, the outer surface glabrate; corolla white, ca. 2 mm long with distinct, short, densely pubescent tube, the limb short and broadly campanulate, the lobes ca. 1 mm long and 0.6 mm wide, with a few glands on outer surface, the inner surface of limb and the bases of filaments with short hairs. *Achenes* ca. 2 mm long, glabrous; carpopodium asymmetric with sigmoid trace; pappus lacking.

FIGURE 30. *Piqueria trinervia* Cav.—A. Habit (× 2/5).—B. Base of plant (× 2/5).—C. Head (× 4).—D. Achene with style (× 2 1/5).—E. Corolla (× 2 1/5).

Piqueria trinervia is widely distributed in Mexico and Central America and occurs on the island of Hispaniola. Distinctive characters of the species include the restricted pubescence of the stems, the glabrous involucral bracts, and the contorted base of the achene.

CHIRIQUÍ: Volcán de Chiriquí, 10,400 ft, *Davidson 1016* (F, MO, US). Loma Larga to summit, Volcán de Chiriquí, ca. 2500–3380 m, *Woodson et al. 1044* (MO, US).

30. SCIADOCEPHALA

Sciadocephala J. Mattfeld, Notizbl. Bot. Gart. Berlin-Dahlem 14: 41. 1938. TYPE: *S. schultze-rhonhofiae* J. Mattfeld.

Small to medium-sized perennial *herbs*, procumbent to erect, the bases usually decumbent, with few or no branches, usually sparsely puberulous on stems, branches of inflorescence, involucre bracts, and corollas, hairs often reddish; stems fistulose. *Leaves* opposite, distinctly petiolate; blades narrowly ovate to elliptical or slightly obovate, the base cuneate to rounded or subtruncate, 2–5 pairs of secondary veins with basal pair often prominent and strongly ascending, the apex narrowly rounded or obtuse to slightly acuminate. *Inflorescence* monocephalic to laxly subcymose with few heads, the ultimate branches elongate. *Heads* discoid with ca. 9–15 florets; involucre of 6–14 eximbricate bracts, in 1–2 series, separated to base, spreading when mature, margin scarious; receptacle scarcely convex, covered with discrete oval scars separated by soft tissue, glabrous; corolla narrowly funnelform with sparse hairs on outer surface, the lobes 4, nonpapillose except on margins, cells of limb with thin somewhat sinuous walls; anther collars stout, not enlarged below, without quadrate cells, with prominent annular thickenings, the exothecial cells quadrate to broader than long, the anther appendage about as long as wide or longer; style base glabrous, not enlarged, style shaft without hairs, the style appendages long and narrow, rounded apically, somewhat soft with thin-walled cells. *Achene* narrowly prismatic, nearly terete, without distinct ribs; carpopodium only slightly asymmetrical, not enlarged, not sharply demarcated above, the cells quadrate; pappus of 5 terete clavate knobs, the knobs with a short globular mass of glutiniferous glands apically. *Pollen* with short spines.

Sciadocephala is a genus of 4 known species occurring mostly in lowland areas of northern South America. The glanduliferous knobs of the achene and the soft tissue between the areoles of the receptacle mark the genus as a close relative of *Adenostemma*. *Sciadocephala* was revised by King & Robinson (1974) but the one Panamanian species has been described since that treatment.

Literature:

King, R. M. & H. Robinson. 1974. Studies in the Eupatorieae (Asteraceae). CXXVII. Additions to the American and Pacific Adenostemmatinae. *Adenostemma*, *Gymnocoronis* and *Sciadocephala*. Phytologia 29: 1–20.

1. **Sciadocephala dressleri** R. M. King & H. Robinson, Phytologia 29: 343. 1975. TYPE: Panama, El Llano—Cartí hwy. *Dressler 4671* (MO, holotype; US, isotype).—FIG. 31.

Decumbent perennial *herb* to 0.5 m tall with few or no branches; stems terete with weak striations, reddish-puberulous. *Leaves* opposite; blades elliptical to slightly obovate, mostly 10–12 cm long and 5–6 cm wide, remotely subserrulate, the base narrowly cuneate, strongly trinervate from near base with strongly ascending secondary veins remote from margin, the apex obtuse to narrowly

rounded, the surfaces mostly glabrous, the veins sparsely puberulous below; petioles 7–25 mm long, distally indistinct from blade. *Inflorescence* laxly subcymose, the branches puberulous, the ultimate branches 1–2 cm long. *Heads* ca. 8–10 mm high and to 1 mm wide with ca. 9 florets; involucral bracts 7–8, eximbricate, in 1 series, narrowly oblong, mostly 2.5–3.5 mm long and to 3 mm wide, apically rounded to obtusely acute, sparsely puberulous on outer surface; corolla pale green, 5.0–5.5 mm long, narrowly funnelform, without distinct tube, sparsely puberulous on outer surface, the lobes 5, ca. 0.7 mm long and 0.5 mm wide; anther collars ca. 0.4 mm long, the thecae ca. 1.5 mm long, the appendage about as long as wide; style branches exserted to 4 mm, cream-colored. *Achenes* to 6 mm long, sparsely minutely puberulous; carpopodium not enlarged; pappus of 5 glutiniferous knobs 1.0–1.5 mm long, the glandular portions ca. 0.2 μ in diameter. *Pollen* ca. 30 μ in diameter.

Sciadocephala dressleri is known only from the type locality in central Panama. The species is most closely related to the type species of the genus, *S. schultze-rhonhofiae*, of western Ecuador. The Ecuadorian species differs primarily by its more erect habit and its more serrate, sharply pointed, elliptical leaf blades. In addition, the involucral bracts and corolla lobes of the type species are slightly more elongate.

PANAMÁ: El Llano–Cartí highway, ca. 12 km N of El Llano, *Dressler 4671* (MO, US).

31. STEVIA

Stevia Cav., Icon. Descr. Pl. 4: 32. 1797. TYPE: *S. serrata* Cav. (see King & Robinson, 1969).

Mustelia Spreng., Nacht. 1, Bot. Gart. Halle 28. 1801. TYPE: *M. eupatoria* Spreng.
Nothites Cass., Dict. Sci. Nat. 35: 163. 1825. TYPE: *N. latifolia* Cass. = *Stevia melissaefolia* (Lam.) Schultz-Bip.
Xetoligus Raf., New Fl. Bot. N. Amer. 4: 74. 1836. TYPE: *Stevia salicifolia* Cav.

Mostly erect annual or perennial *herbs* or *shrubs*, sparingly to densely branched. *Leaves* opposite or alternate, sessile to distinctly petiolate; blades linear to orbicular, the margins entire to serrate or dentate, rarely deeply lobed, the surface usually puberulous or stipitate-glandular, usually glandular punctate. *Inflorescence* diffuse with few long-pedunculate heads or dense in corymbose panicles. *Heads* discoid with 5 florets; involucre narrowly cylindrical; involucral bracts 5, eximbricate, in 1 series, linear to elliptical, easily torn from receptacle; receptacle glabrous; corolla narrowly funnelform or with somewhat expanded throat, usually with hairs or glands on outer surface and with hairs on inner surface, the cells of the limb elongate with sinuous walls, the lobes rarely to 2 mm long, shorter than throat and tube, oblong-ovate, sometimes zygomorphic with outer lobes longer, densely papillose on inner surface, smooth on outer surface; anther collars cylindrical to larger below, with many quadrate to short-oblong cells below, the cell walls with variably annulate thickenings, the exothecial cells subquadrate to short-oblong, the anther appendage mostly obovate with prominently crenulate distal margin; style base with distinct enlargement, glabrous, or in a few species papillose, the style appendages filiform, densely

FIGURE 31. *Sciadocephala dressleri* R. M. King & H. Robinson.—A. Habit (× ½).—B. Head (× 4½).—C. Stamen (× 23).

long-papillose. *Achenes* fusiform to cylindrical, strongly 5-ribbed with few to many glands or bristles; carpopodium distinct, short, slightly asymmetric with a few rows of small quadrate to short-oblong cells; pappus with at least a crown of free to united scales, often with 1–30 awns or bristles; one of the achenes in each head often with more reduced pappus. *Pollen* with short spines, sometimes with complex furrows or cylindrical to dumbbell shaped.

The genus *Stevia* contains about 150–200 species (Grashoff, 1972) and ranges from the southwestern United States through Mexico, Central America, and South America to Argentina. Four species have been collected in Panama.

Literature:

Grashoff, J. L. 1972. A systematic study of the North and Central American species of *Stevia*. Ph.D. dissertation, University of Texas. 608 pp. Microfilm 73-7556.

King, R. M. & H. Robinson. 1967. Multiple pollen forms in two species of the genus, *Stevia* (Compositae). Sida 3: 165–169.

——— & ———. 1968. Studies in the Compositae-Eupatorieae. VIII. Observations on the microstructure of *Stevia*. Sida 3: 257–269.

Robinson, B. L. 1930a. Observations on the genus *Stevia*. Contr. Gray Herb. 90: 36–58.

———. 1930b. The Stevias of North America. Contr. Gray Herb. 90: 90–160.

a. Shrub; leaves glabrous, the veins pinnate; corolla lobes glabrous on outer surface .. 2. *S. lucida*
aa. Perennial herbs or subshrubs; leaves puberulous at least on veins, the veins weakly to strongly trinervate; corolla lobes with few to many hairs on outer surface.
b. Pedicels and involucral bracts with few to many stipitate glandular hairs ..... 1. *S. caracasana*
bb. Pedicels and involucral bracts with only nonglandular hairs and glandular punctations.
c. Leaves puberulous to subtomentose on lower surface; involucral bracts long-acute or slightly acuminate, scarcely scarious at tips; achenes without pappus awns ..... 4. *S. triflora*
cc. Leaves puberulous only on veins of lower surface; involucral bracts usually short-acute, often broadly scarious at tips; usually some achenes with 1–2 pappus awns ..... 3. *S. ovata*

1. **Stevia caracasana** DC., Prodr. 5: 121. 1836. TYPE: Venezuela, near Caracas, *Vargas 108* (G-DC, not seen, US, microfiche).

S. elliptica Hook. & Arn., Bot. Beech. Voy. 424. 1841. TYPE: Mexico, between San Blas and Tepic, Nayarit, *Sinclair* (K, holotype, not seen).
S. hirtiflora Schultz-Bip., Linnaea 25: 274. 1853. TYPE: Mexico, near Regla, Hidalgo, *Ehrenberg 30* (P, holotype, not seen).
S. elongata var. *caracasana* (DC.) B. L. Robinson, Contr. Gray Herb. 90: 141. 1930.

Unbranched or sparingly branched rhizomatous perennial *herbs;* stems often brownish or purple, terete, slightly striate, densely puberulous. *Leaves* opposite; blades ovate, 3–10 cm long and 2–5 cm wide, the base cuneate or rarely subtruncate, usually abruptly decurrent onto petiole, the margins serrate to serrulate, the apex usually short-acute to obtuse, the surfaces with glandular punctations, the upper surface glabrous to sparsely short-pilose, the lower surface sparsely

puberulous to pilose along veins, glabrous or scarcely puberulous on areoles, the veins distinctly trinervate near base; petioles 5–10 mm long, winged distally, sometimes indistinct from lamina. *Inflorescence* usually laxly paniculate, the primary branches opposite, often spreading at more than 45°, densely corymbose terminally, densely puberulous to pilose with few to many stipitate glandular hairs, the ultimate branches mostly 0–3 mm long, rarely to 7 mm long; subinvolucral bracts sometimes broadly elliptical to ovate and prominent. *Heads* ca. 7–10 mm high; involucral bracts mostly narrowly oblong-lanceolate, mostly ca. 6 mm long and 1.2 mm wide, slightly striate, with some glandular punctations, puberulous, with few to many stipitate glandular hairs, the apex usually sharply acute, the margins scarcely scarious; corolla pink or pinkish, 5–6 mm long, hirsute mostly on lobes and limb, with scattered minute glandular punctations, the lobes equal, ca. 1 mm long. *Achenes* 3.5–4.0 mm long, short- to long-hispid; pappus a low, serrate crown of united scales 0.1–0.3 mm long, 4 achenes of head often bearing 3 barbellate basally winged awns alternating with scales.

Stevia caracasana is distributed from central Mexico southward through Central America to Colombia and Venezuela. The species is similar to *S. ovata* but can be distinguished by the stipitate glandular hairs on the branches of the inflorescence and on the involucral bracts. Fully developed specimens of the species can also be distinguished by the more thyrsoid paniculate inflorescences with shorter more spreading lateral branches.

CHIRIQUÍ: Pastures around El Boquete, 1000–1300 m, *Pittier 2865* (US). COCLÉ: Picacho de Olá, 350–600 m, *Pittier 5073* (US).

2. **Stevia lucida** Lag., Gen. Sp. Pl. Nov. 28. 1816. TYPE: Mexico, Ixmiquilpan and Zimapán (Cimmapan), Hidalgo, *Née* (MA, not seen).—FIG. 32.

S. *glutinosa* H.B.K., Nov. Gen. Sp. Pl. 4: 116. ed. fol. 1818. TYPE: Colombia, near Santa Fe de Bogotá and Suacha, *Humboldt & Bonpland* (P, not seen, US, microfiche).

S. *fastigiata* H.B.K., Nov. Gen. Sp. Pl. 4: 116. ed. fol. 1818. TYPE: Mexico, near city of Guanajuato, *Humboldt & Bonpland* (P, not seen, US, microfiche).

? S. *nitida* Walp., Linnaea 14: 320. 1840. TYPE: Mexico, without precise locality, *Karwinski* (LE?, not seen).

S. *grandidentata* Schultz-Bip. ex Klatt, Leopoldina 20: 75. 1884, not S. *grandidentata* Schultz-Bip., Bull. Soc. Bot. France 12: 81. 1865. TYPE: Mexico, Tehuacán, Puebla, *Liebmann 126* (P, holotype, not seen).

S. *oaxacana* Schultz-Bip. ex. Klatt, Leopoldina 20: 75. 1884, nom. nud.

Shrubs to 2 m tall with few to many branches, with stems, leaves, branches of inflorescence and involucral bracts vernicose; stems mostly brown, terete or slightly hexagonal, internodes often short, usually glabrous. *Leaves* opposite; blades oblong-ovate to lanceolate, to 16 cm long and 5 cm wide, somewhat conduplicate, the base cuneate or rarely subtruncate, the margins regularly serrate or crenate to remotely dentate, the apex shortly to narrowly acute or slightly acuminate, the surfaces densely glandular-punctate, the lower surface pale and more fleshy; the veins pinnate or with lower pair slightly more prominent; petioles to 2 cm long, wings not obvious. *Inflorescence* flat-topped, corymbose, with lower branches opposite or alternate, the branches puberulous, the ultimate branches 0–2 mm long. *Heads* mostly 9–11 mm high; involucral bracts narrowly oblong-elliptical, 5–6 mm long and 0.7–1.5 mm wide, glandular-punctate, the

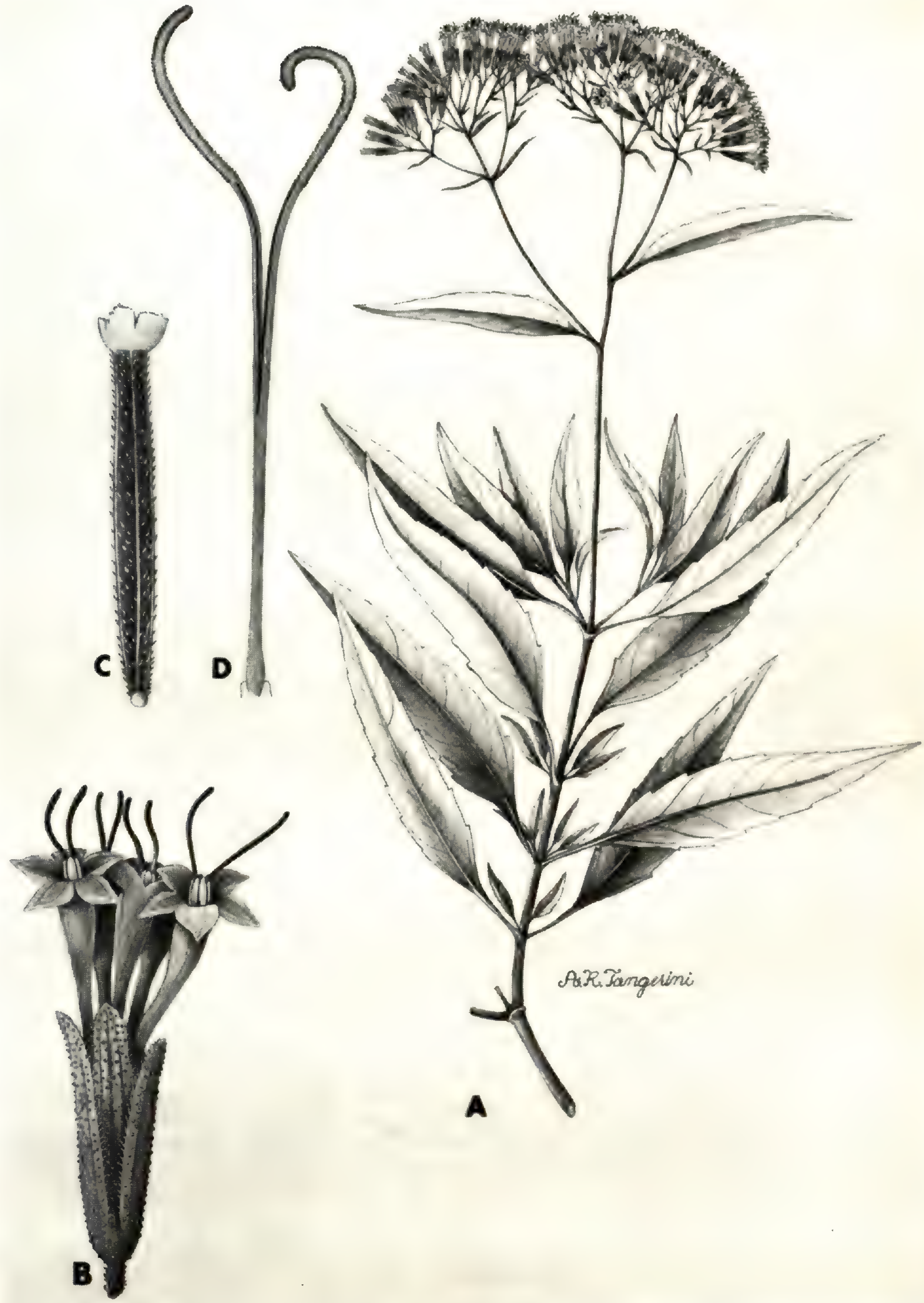

FIGURE 32. *Stevia lucida* Lag.—A. Habit (× ½).—B. Head (× 5).—C. Achene (× 10).—D. Style (× 10).

apex usually acute and somewhat scarious; corolla pink, 5–6 mm long, glandular-punctate with hairs on lower parts, the lobes equal, 1.0–1.2 mm long, glabrous. *Achenes* 3.5–5.5 mm long, hispid, rarely with some glands; pappus a low crown of dentate to entire, united or separate scales, 0.2 mm high, without awns.

Stevia lucida is widely distributed from central Mexico southward through Central America to the northern Andes in Colombia and Venezuela. The species is one of the most distinct in the genus with glabrous vernicose leaves, stems, and involucral bracts. The species is the only member of the series *Fruticosae* in Panama, but the shrubby habit difference is not always evident in herbarium specimens. The Panamanian material of the species is all of the variety *oaxacana* (DC.) Grashoff which has the branches of the inflorescence subopposite or alternate.

CHIRIQUÍ: Llano del Volcán, 4500 ft, *Allen 4854* (MO). Llano del Volcán, 1500–1600 m, *Allen & Fairchild 3470* (MO). Volcán de Chiriquí, Potrero Muleto, 10400 ft, *Davidson 1052* (F, US). Between El Hato and Cerro Punta, *Ebinger 801* (F, MO, US). Barú Mtn., 2900 m, *McCorkle C-152* (US). W slope of El Barú, 6000–7000 ft, *Tyson & Loftin* 5959 (FSU, MO). Top of El Barú above 1100 ft, *Tyson & Loftin 6178* (FSU). Río Chiriquí Viejo valley, near El Volcán, *White 207* (MO, US). NE of El Hato del Volcán, near Aguacate, 1800–1900 m, *Wilbur et al. 10978* (MO, US). 5 mi NE of El Hato del Volcán towards Volcán de Chiriquí, *Wilbur et al. 11870* (F, MO).

3. **Stevia ovata** Willd., Enum. Pl. Hort. Berol. 855. 1809. TYPE: Material and name perhaps from Lagasca (see below).

S. *ovata* Lag., Gen. Sp. Pl. Nov. 27. 1816. TYPE: Cultivated, originally from Mexico, *Née* (MA, not seen).
S. *paniculata* Lag., Gen. Sp. Pl. Nov. 27. 1816. TYPE: Cultivated, origin Mexico, *Née* (MA, not seen).
S. *rhombifolia* H.B.K., Nov. Gen. Sp. Pl. 4: 112. ed. fol. 1818. TYPE: Mexico, Mt. Sanctae Guadalupe near Mexico City, *Humboldt & Bonpland* (P, not seen, US, photo).
S. *quitensis* H.B.K., Nov. Gen. Sp. Pl. 4: 113. ed. fol. 1818. TYPE: Ecuador, between Quito and Mt. Burro Potrero, *Humboldt & Bonpland* (P, not seen, US, microfiche).
S. *ternifolia* H.B.K., Nov. Gen. Sp. Pl. 4: 115. ed. fol. 1818. TYPE: Mexico, Michoacán, *Humboldt & Bonpland* (P, not seen, US, microfiche).
S. *fascicularis* Less., Linnaea 5: 140. 1830. TYPE: Mexico, near Jalapa and near Hacienda de la Laguna, *Schiede & Deppe 198* (W, not seen, US, photo).
S. *nervosa* DC., Prodr. 5: 117. 1836. TYPE: Mexico, near Villalpando to east of Guanajuato, *Mendez* (G-DC, not seen, US, photo).
S. *uniaristata* DC., Prodr. 5: 120. 1836. TYPE: Mexico, in mountains near León, west of Guanajuato, *Mendez* (G-DC, not seen, US, photo).
S. *reglensis* Benth., Pl. Hartw. 40. 1840. TYPE: Mexico, Regla, Hidalgo, *Hartweg 808* (K, holotype, not seen; NY, P, isotypes, not seen; G, isotype, not seen, US, photo).
S. *ehrenbergiana* Schlechter, Linnaea 16: 370. 1842. TYPE: Mineral del Monte, *Ehrenberg* (B, destroyed; HAL, not seen).
S. *benthamiana* Hieron, Bot. Jahrb. Syst. 28: 561. 1901. TYPE: Ecuador, Guapulo bridge near Quito, *Hartweg 1090* (P, not seen; NY, not seen; K, not seen, US, photo).

Sparingly branched rhizomatous perennial *herbs*; stems often brownish or purple, terete, slightly striate, densely puberulous. *Leaves* opposite; blades ovate to oblong-elliptical, 3–9 cm long and 1.5–5.0 cm wide, the base cuneate and decurrent onto petiole, the margins entire to serrate, the apex obtusely to sharply acute, the surfaces glandular punctate, the upper surface glabrate to sparsely puberulous, the lower surface puberulous on veins, glabrous or scarcely puberulous on areoles, the veins distinctly trinervate from near base; petioles 2–25 mm long,

winged and often distally indistinct from lamina. *Inflorescence* usually flat-topped and densely corymbose, the primary branches opposite, usually spreading at less than 45°, the branching sometimes diffuse, the branches densely puberulous to subtomentose, the ultimate branches 0–2 mm long, rarely to 8 mm long. *Heads* 6–8 mm high; involucral bracts narrowly oblong, mostly 4–5 mm long and 0.7–1.0 mm wide, glandular punctate, distinctly puberulous, the apex often short-acute or prominently scarious; corolla white or rarely slightly pink, 4.5–5.5 mm long, glandular punctate, with short hairs on tubes and few on limb, the lobes equal, 0.7–1.2 mm long with many multiseptate hairs on outer surface. *Achenes* ca. 3 mm long, sparsely short-hispid; pappus with a crown of separate to united scales ca. 0.3–1.0 mm high, subentire to dentate, with 0–4 barbellate, basally winged awns ca. 4 mm long, often alternating with scales.

Stevia ovata is distributed from northern Mexico southward through Central America to the Andes in Venezuela and Ecuador. Some of the Panamanian specimens have a diffuse habit with small lax corymbs or single long pedunculate heads. Such plants seem to occur sporadically in the species. Pappus awns are usually common in the species but sometimes are lacking from most heads. Still, awns have been seen in a few heads of almost every specimen examined.

CHIRIQUÍ: Boquete–Salta and Volcancitos, 5500 ft, *Davidson 1265* (F, MO). Volcán, ca. 4600 ft, *Duke 9152* (MO, OS, US). Boquete district, 4500 ft, *Terry 1275* (F, US). 3 mi N of El Volcán, 5000 ft, *Tyson 5859* (FSU, MO).

4. **Stevia triflora** DC., Prodr. 5: 115. 1836. TYPE: Mexico, San Felipe, Oaxaca, *Karwinski* (G-DC, not seen, US, microfiche; M, not seen, US, photo).

S. compacta Benth., Pl. Hartw. 197. 1845. TYPE: Colombia, near Río Negro between villages of Fusagasugá and Pandi, *Hartweg 1091* (K, holotype, not seen).

S. rhombifolia var. *stephanocoma* Schultz-Bip., Linnaea 25: 279. 1853. TYPE: Venezuela, Mérida, "Colombia," *Moritz 1375* (P, holotype, not seen).

Sparingly branched rhizomatous perennial *herbs*; stems mostly brownish, never purple, terete, slightly striate, densely puberulous. *Leaves* opposite; blades ovate to narrowly ovate, 4–8 cm long and 2–5 cm wide, the base cuneate and decurrent onto petiole, the margins slightly to closely serrate or serrulate, the apex acute, the surfaces glandular punctate, the upper surface puberulous, the lower surface puberulous to tomentose on veins and areoles, the veins distinctly trinervate from near base; petioles usually 0.5 cm long, winged and sometimes distally indistinct from lamina. *Inflorescence* flat-topped, densely corymbose, the primary branches opposite, usually spreading at less than 45°, branches densely puberulous to subtomentose, the ultimate branches 0–2 mm long. *Heads* ca. 6–7 mm high; involucral bracts narrowly oblong-lanceolate, 4.5–5.5 mm long and 0.7 mm wide, slightly striate, minutely glandular-punctate, scarcely scarious on margins; corolla white, ca. 4.5 mm long, glandular punctate with few short hairs on tubes and lobes, the lobes equal, ca. 1.2 mm long. *Achenes* 2.5–3.0 mm long, sparsely hispid; pappus a fimbrillate to subentire crown of united scales ca. 0.3 mm long, without awns.

Stevia triflora is distributed from central Mexico southward through Central America to the Andes in Ecuador. The species seems close to the common *S. ovata*

and is placed in synonymy by some authors. Some specimens, especially from Chiapas southward, are difficult to distinguish. The pubescence of the lower leaf surface and the complete lack of pappus awns seem the most useful characters. Plants thusly distinguished show a more sharply acute and less scarious tip on the involucral bracts than is seen in most specimens of *S. ovata*.

CHIRIQUÍ: Cerro Vaca, 900–1136 m, *Pittier* 5297 (US). Valley of the upper Río Chiriquí Viejo, *White & White 106* (MO). PANAMÁ: Beyond Goofy Lake along road to Cerro Jefe, *Correa & Dressler 451* (MO).

32. TUBEROSTYLIS

Tuberostylis Steetz in Seem., Bot. Voy. Herald 142. 1853. TYPE: *T. rhizophorae* Steetz.

Creeping to scandent small *shrubs*, moderately branched; stems terete, frequently rooting at nodes. *Leaves* opposite, distinctly petiolate; blades slightly succulent, obovate to elliptical, the bases cuneate, the margins entire to crenulate, the apex obtuse to short-acuminate, the veins trinervate from near base. *Inflorescence* terminal on lateral branches or sessile at nodes, corymbose or in subglobose clusters. *Heads* discoid with ca. 10–20 florets; involucre of ca. 25–35 subimbricate bracts, in 4–5 series, very unequal, distinctly striate on outer surface, the outer bracts spreading when mature, the inner bracts deciduous; receptacle flat or slightly convex, glabrous; corolla narrowly tubular with slightly thickened base, the lobes 5, short, nonpapillose, with few or no glands, the corolla cells elongate with sinuous walls; anthers elongate, broad, with mostly short-oblong cells, the cell walls with weak annulate thickenings, the exothecial cells subquadrate, the anther appendage about as long as wide; style base not enlarged, glabrous, the style appendages linear, slightly mamillose. *Achenes* prismatic to cylindrical, covered with thick rind of hyaline cells when mature, glabrous; carpopodium short, indistinct; pappus lacking. *Pollen* with short sharp spines.

Tuberostylis is a genus of 2 species distributed mostly along the Pacific coast of northern South America. One species has been collected in Panama.

1. **Tuberostylis rhizophorae** Steetz in Seem., Bot. Voy. Herald 142. 1853. TYPE: Panama, epiphytic on roots of mangrove trees, southern Darién, *Seemann 2201* (BM, not seen, US, photo).—FIG. 33.

Creeping, much branched, often epiphytic small *shrubs*; stems becoming dark brown, slender, slightly fleshy, glabrous. *Leaves* opposite, fleshy; blades obovate to rhomboidal, to 2.5 cm long and 1.8 cm wide, the base cuneate, abruptly narrowly decurrent, the margins slightly crenate in distal half or two-thirds, the apex rounded to obtuse, the surfaces glabrous, the veins obscurely trinervate near base; petioles to 2.5 cm long, with slender bases, becoming slightly but distinctly broader distally. *Inflorescence* terminal on lateral branches, slightly corymbose, the branches sparsely puberulous. *Heads* sessile or nearly sessile in clusters of 2–4, 8–9 mm high and ca. 3 mm wide with 10–12 florets; involucral bracts 25–30, imbricate, in ca. 5 series, 1–7 mm long, short-orbicular to oblong with rounded scarious tips, the outer surface glabrous with 3–5 striations; corolla white, ca. 3.5

FIGURE 33. *Tuberostylis rhizophorae* Steetz.—A. Habit (× ½).—B. Head (× 5⅖).—C. Corolla (× 12³⁄₁₀).—D. Achene (× 12³⁄₁₀).—E. Style (× 12³⁄₁₀).

mm long, tubular, the lobes short, about as wide as long, glabrous; style branches scarcely broader distally, slightly mamillose. *Achenes* ca. 3 mm long, prismatic to cylindrical, becoming thickly corticated by layers of thin-walled whitish cells at maturity; carpopodium not distinct; pappus lacking. *Pollen* ca. 23 μ in diameter.

The species was originally described from Panama but only one recent collection has been seen from the country. The species is most common in the mangrove areas along the Pacific coast of Colombia and the range extends south into Ecuador.

DARIÉN: Río Piñas, *Duke 10556* (MO).

III. ASTEREAE

W. G. D'ARCY[10]

Astereae Cass., Jour. Phys. 88: 195. 1819. TYPE: *Aster* L.

Asteroideae Less., Linnaea 5: 142. 1830. TYPE: *Aster* L.

Mostly perennial, sometimes annual, *herbs* occasionally *shrubs*, rarely *trees*. *Leaves* mostly alternate, entire or toothed but seldom deeply dissected. *Inflorescences* various. *Heads* disciform or radiate with one to several marginal series of mostly fertile pistillate florets and few or numerous, fertile or sterile, staminate or hermaphrodite florets in the center, sometimes unisexual (when dioecious); involucral bracts imbricate in several similar or unlike series, mostly with a narrow hyaline margin, often apically erose; receptacle naked or rarely with persistent or deciduous paleas, alveolate, muricate, or smooth, flat to conical; ray florets mostly with an apically 3-dentate or entire ligule, or the ligule wanting and the apex truncate, erose, or denticulate, anthers lacking, styles mostly linear, sometimes dorsally grooved, mostly glandular; disc florets yellowish, campanulate-crateriform, apically 5-dentate, anthers apically appendaged, truncate, obtuse or minutely auricled basally, style branches flattened, glandular on the margins, mostly apically appendaged with deltoid to lanceolate glandular appendages, or if the appendages not apparent then the branches fusiform and dorsally glandular overall, rarely undivided (sterile florets). *Achene* mostly laterally flattened, the margins mostly thickened by nerves, glabrous or pubescent, sometimes stipitate or beaked; pappus mostly of fine strigose bristles in 1–3 series, rarely of scales or wanting, rarely supplanted by a glandular beak or rim, rarely plumose.

This tribe includes over 1400 species in over 90 genera of cosmopolitan distribution (Bentham, 1873). The laterally compressed achenes and usually radiate or disciform heads are conspicuous unifying features.

Literature:

Cuatrecasas, J. 1969. Prima Flora Colombiana 3. Compositae-Astereae. Webbia 24: 1–335.

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[10] Missouri Botanical Garden, 2315 Tower Grove Avenue, St. Louis, Missouri 63110.

a. Heads radiate; ligules manifestly exceeding the stigmas, pappus, and inner or disc florets.
  b. Pappus wanting, replaced by a sticky glandular peg; heads borne singly on scapes to 12 cm tall ..... 38. *Lagenifera*
  bb. Pappus of fine bristles; heads several to many on stems or branches often more than 12 cm tall.
    c. Midvein of involucral bracts slightly enlarged apically; leaves reduced to scales or spines ..... 34. *Aster*
    cc. Midvein of involucral bracts not enlarged apically; leaves not reduced to scales or spines ..... 37. *Erigeron*
aa. Heads disciform; ligules absent or not exceeding the stigmas, pappus, and inner or disc florets.
  d. Heads all alike, perfect, and fertile; pistillate (outer) florets cylindrical or broadening upward; staminate (inner) florets shallowly lobed, the limb indistinct or tubular; herbs ..... 36. *Conyza*
  dd. Heads structurally or functionally unisexual; pistillate (outer or all) florets cylindrical or narrowing upward; staminate (inner or all) florets deeply lobed (nearly halfway or more), the limb clearly expanded and campanulate or tubular; shrubs, trees, or woody vines.
    e. Leaves coriaceous, 3(–7)-nerved from the base, the margins entire; plants functionally and structurally dioecious; receptacle muricate; pistillate florets inflated near the base and narrowing upward ..... 35. *Baccharis*
    ee. Leaves not coriaceous, pinnately nerved, the margins mostly callose-denticulate; plants functionally dioecious but at least the pistillate heads with florets of the opposite sex; receptacle smooth or alveolate; pistillate florets narrowing abruptly at the extreme base and not narrowing upward ..... 33. *Archibaccharis*

33. ARCHIBACCHARIS

Archibaccharis Heering, Jahrb. Hamburg Wiss. Anst. Beih. 21(3): 40. 1904. LECTOTYPE: *A. hieraciifolia* Heering.

Hemibaccharis Blake, Contr. U. S. Natl. Herb. 20: 552. 1924. TYPE: *H. hieracioides* Blake.

Herbs or weak, often divaricate, scandent *shrubs* to 4(–10) m tall, mostly pubescent; stems often striate, sometimes fistulose. *Leaves* alternate, membranaceous or chartaceous, dentate in the upper portion or subentire with toothlike, well spaced, callose mucros, pinnately veined, mostly pubescent, sometimes glandular, rarely scabrous; petioles mostly short or wanting. *Inflorescence* a panicle, often rounded, open or compact; reduced, leaflike bracts and scalelike bracteoles mostly present; pedicels filiform. Plants dioecious, perhaps sometimes polygamous; *heads* disciform, mostly with pistillate outer florets and hermaphrodite inner florets but only one sex fertile on a plant; involucral bracts imbricate, in several unequal and unlike series, the innermost lanceolate, glabrous with a slender midvein, the outer series broader, often pubescent with a broader midvein, the hyaline margins apically erose and flanking an indurated stramineous region; receptacle flat, naked, smooth or alveolate; outer florets slender or capillary, the corolla cylindrical, hardly expanded at the base, apically truncate, erose, denticulate or with a small ligule, often pubescent upwards, the style exserted, its branches slender, mostly elongate, glandular, the ovary compressed, pubescent, more so at the base, the pappus of fine strigose bristles in one series; inner florets with crateriform corollas, the corolla tube and base of the limb mostly pubescent, the limb tubular or campanulate, 5-lobed, sometimes deeply so, the lobes acute or ensiform with thickened margins, mostly glabrous, the anthers auricled on the

inner (ventral) side, the appendages lanceolate, the style sometimes pubescent, its branches elongate, fusiform, glandular-papillose dorsally, mostly exserted from the anther appendages, the ovary sterile, mostly shrunken, the pappus slightly expanded apically. *Achene* compressed, often pubescent.

Archibaccharis is distinct in being dioecious while having sterile florets of the opposite sex in at least the pistillate heads. The leaves of most species are also distinctive in the minute teeth of callose mucros which stand at a prominent angle to the leaf margin. The genus differs from *Baccharis* in mostly lacking coriaceous leaves, in possessing two kinds of florets in the heads, in the presence of flat, smooth, or alveolate receptacles, and in the absence of a conspicuous swelling at the base of the corolla of the outer (pistillate) florets. *Archibaccharis* is also closely related to *Conyza* and *Erigeron*. Two interesting features possessed by the genus are the minute auricles on the inner (ventral) surfaces of the anther bases and the tendency of the staminate florets to change from white to rose or purplish in age, colors unusual in disc florets in this tribe.

This is a genus of about 20 species ranging from Mexico to Panama. The three Panamanian species are all from middle and upper elevations.

Literature:

Jackson, J. D. 1975. Revision of the genus *Archibaccharis* Heering (Compositae-Astereae). Phytologia 32: 81–194.

a. Styles of capillary outer florets exserted less than ⅓ their length; inner florets mostly more than 3.5 mm long; leaves mostly more than 3 times as long as broad.
   b. Capillary outer florets apically erose or truncate, without a defined ligule; veins 6 or more on each side of the midvein; limb of the inner crateriform florets divided less than halfway ——— 1. *A. irazuensis*
   bb. Capillary outer florets with a definite ligule ca. 1 mm long; veins ca. 5 on each side of the midvein; limb of the inner crateriform florets divided deeply —— 2. *A. panamensis*
aa. Styles of capillary outer florets exserted half their length or more; inner florets mostly less than 3.5 mm long; leaves mostly less than twice as long as broad ——— 3. *A. schiedeana*

1. **Archibaccharis irazuensis** (Blake) Blake, Jour. Wash. Acad. Sci. 17: 60. 1927.—FIG. 34 D–E.

Hemibaccharis irazuensis Blake, Contr. U. S. Natl. Herb. 20: 551. 1924. TYPE: Costa Rica, *Pittier 14079* (US, not seen).

Shrub or woody *herb* to 2 m tall; stems smooth or striate, puberulent with weak, spreading, brownish, granular hairs, sometimes glabrescent. *Leaves* to 9 cm long, narrow, elliptic, ovate or lanceolate, basally rounded or narrowed, apically acuminate, the margins denticulate with toothlike, callose mucros, with 6 or more ascending pinnate veins on each side of the midvein, reticulate beneath, pubescent on both sides, more so beneath; petioles short or wanting. *Inflorescence* a flat or rounded terminal panicle to 10 cm across; peduncles and pedicels tomentose; bracts resembling small leaves, the bracteoles scalelike, 3–4 mm long. *Heads* disciform; involucral bracts imbricate in several unequal series, indurate, stramineous, the innermost narrowly lanceolate, 3–4 mm long, the outer series shorter, broader, and dorsally pubescent, the midvein prominent, the apices erose; outer florets 4–5 mm long, the corolla capillary, 1.5–3 mm long, apically erose or

truncate, manifestly pubescent, the style exserted for less than ⅓ its length, its branches linear, somewhat flattened, dorsally papillose, not exceeding the pappus; inner florets 4–5 mm long, the corolla 3–5 mm long, the tube pubescent upwards, the limb basally pubescent, lobed halfway down or less, the lobes obtuse, marginally thickened, glabrous or slightly glandular at the tips, the anthers ca. 1.2 mm long, basally auricled, the appendages narrow, the style branches flattened-fusiform, dorsally papillose-pilose, the ovary shrivelled, the pappus apically expanded. *Achene* flattened, 3-angled, pubescent; pappus of fine strigose bristles in one series.

This species is known only from upland areas of Costa Rica and the Chiriquí mountains. It is closely related to *Archibaccharis serratifolia* (H.B.K.) Blake of Mexico and Guatemala which differs in its much denser, stouter pubescence and its usually much larger leaves.

CHIRIQUÍ: Boquete District, slope of Volcán de Chiriquí, 9500 ft, *Davidson 991* (MO, US). Potrero Muleto to summit, Volcán de Chiriquí, 3500–4000 m, *Woodson & Schery 463* (MO).

2. **Archibaccharis panamensis** Blake, Ann. Missouri Bot. Gard. 28: 472. 1941. TYPE: Panama, *Allen 751* (US, holotype; MO, isotype).—FIG. 34A–C.

Herb or *vine* to 3 m tall; stems evenly striate and pubescent with dense, short, weak, brownish spreading hairs. *Leaves* to 10 cm long, subsessile, elliptical, basally acute, apically slightly acuminate and mucronate, the margins subentire with toothlike, callose mucros, with ca. 6 ascending pinnate veins on each side of the midvein, obscure above, finely reticulate and lighter beneath, pubescent on both sides, above with short scattered hairs, beneath with weak, granular spreading hairs most plentiful on the veins. *Inflorescence* a terminal or axillary, congested or open panicle to 30 cm across; peduncle puberulent, the pedicels to 15 mm long, filiform; bracteoles scalelike. *Heads* white, disciform; involucral bracts imbricate in about 3 unequal series, stramineous, the innermost lanceolate, glabrous, 4 mm long, the outer series mostly herbaceous, shorter, broader, densely pubescent, apically erose; receptacle flat, ca. 1 mm across, naked, muricate; outer florets 4–5 mm long, the corolla 2–2.5 mm long, capillary, apically forming a short, clasping ligule 1 mm long that reaches the base of the style branches, the tube pubescent upwards, pilose at the base of the ligule, the style branches exserted, ca. 1 mm long, flattened, lanceolate, dorsally finely glandular; inner florets ca. 5 mm long, the corolla crateriform, the tube ca. 1 mm long, pubescent overall, the limb basally pubescent, divided nearly to the base into 5 ensiform, marginally thickened lobes, the anthers 0.7 mm long, basally minutely auricled, the appendages lanceolate, the style branches 0.8 mm long, exserted from the anther appendages, fusiform, densely glandular-papillose, the ovary reduced (sterile). *Achene* flattened, 3 angles thickened by veins, densely pubescent; pappus of fine strigose bristles in one series, sometimes apically enlarged.

Archibaccharis panamensis and *A. flexilis* (Blake) Blake of Guatemala are distinctive in the ligulate outer florets which partly envelop the style and in the deeply lobed corollas of the inner florets. *Archibaccharis panamensis* may not in fact be a distinct species, but the inflorescence of the type collection is a large

FIGURE 34. *Archibaccharis*.—A–C. *A. panamensis* Blake.—A. Habit of male plant (× 2/5).—B. Capillary outer floret (× 16).—C. Inner staminate floret (× 16). [After *Allen 751* (MO).]—D–E. *A. irazuensis* (Blake) Blake.—D. Inner staminate floret (× 16).—E. Outer capillary floret (× 16). [After *Woodson & Schery 463* (MO).]

open terminal panicle, while the inflorescences of material considered to be *A. flexilis* from further west is axillary and much smaller.

COCLÉ: Near El Valle, 800–100 m, *Allen 751* (MO, US).

3. **Archibaccharis schiedeana** (Benth.) J. D. Jackson, Phytologia 28: 297. 1974.

Baccharis scandens Less. in Cham. & Schlecht., Linnaea 5: 146. 1830, not Pers., Syn. Pl. 2: 424. 1807. TYPE: Mexico, *Schiede 318* (GH, not seen).
B. schiedeana Benth. in Örst., Vidensk. Meddel. Dansk Naturhist. Foren. Kjøbenhavn 1852: 83. 1852, new name for *B. scandens* Less.
Hemibaccharis torquis Blake, Contr. U. S. Natl. Herb. 20: 550. 1924. TYPE: Costa Rica, *Tonduz 1535* (US, not seen).
H. salmeoides Blake, Contr. U. S. Natl. Herb. 20: 5. 1926. TYPE: Guatemala, *von Tuerckheim II1641* (MO).
Archibaccharis torquis (Blake) Blake, Contr. U. S. Natl. Herb. 23: 1508. 1926.

Shrub or woody *vine* festooning in thickets to 10 m tall, the branching divaricate; stems leafy, puberulent with weak granular hairs, drying evenly striate, fistulose. *Leaves* to 10 cm long, elliptical or ovate, basally acute or short-acuminate, apically acute or acuminate, mostly mucronate, the margins denticulate with toothlike, callose mucros, ca. 5 pinnate veins ascending on each side from near the base of the midvein, puberulent on both sides with short weak hairs and subsessile glands; petioles to 10 mm long, slender, tomentose. *Inflorescences* numerous, slightly congested ternately divided panicles or cymes, often round topped; peduncles tomentose; bracts similar to reduced leaves; pedicels to 8 mm long, filiform; bracteoles scalelike. *Heads* disciform, 4–5 mm tall, the staminate heads slightly shorter; involucral bracts imbricate in several unequal series, indurate, stramineous, the innermost narrowly lanceolate, 4–5 mm long, the outer series shorter, broader and dorsally puberulent, the green midvein prominent, the apices erose, often purplish; outer florets 4 mm long, the corolla white, sub-cylindrical, narrowed upward, apically truncate, oblique or erose, glabrous or sparingly pubescent near the top, the style exserted for more than half its length, its branches ensiform, ca. 1 mm long, smooth; inner florets 2.5–4 mm long, the corolla white, crateriform, the tube pubescent upwards, the limb basally pubescent, deeply lobed, the lobes ensiform, marginally thickened, the anthers exserted, 1.5 mm long, basally auricled, the appendages narrow, the style scarcely exserted from the anther appendages, its branches flattened-fusiform, dorsally glandular papillose, the ovary much reduced in length, the pappus sometimes flattened basally or expanded apically. *Achene* a flattened wedge, the three angles thickened by prominent veins, copiously pubescent and with a ring of bristles at the base; pappus of fine strigose bristles in one series.

This species is distinct in its scandent habit, the small broad leaves, the often purplish-tipped involucral bracts, and the short outer florets with long-exserted styles. The inner florets are mostly less than 3.5 mm long.

Archibaccharis schiedeana ranges from Panama to Mexico. It is known in Panama only from the Chiriquí mountains.

CHIRIQUÍ: Río Chiriquí Viejo N of Volcán, 5200–5600 ft, *Duke 9042* (MO). Pastures around Boquete, *Pittier 2855* (US). Volcán de Chiriquí, Boquete District, 5000 ft, *Terry 1363* (MO). Near Callejón Seco, Volcán de Chiriquí, 1700 m, *Woodson & Schery 481* (MO).

34. ASTER

Aster[11] L., Sp. Pl. 872. 1753; Gen. Pl., ed. 5. 373. 1754. TYPE: *A. amellus* L.

Leucosyris E. L. Greene, Fl. Francisc. 384. 1891. TYPE: *L. carnosa* (A. Gray) E. L. Greene.

Annual or perennial, mostly erect *herbs*, sometimes spreading by rhizomes; the stems often much branched, occasionally woody. *Leaves* alternate, mostly entire or nearly so and well spaced along the stems, usually becoming smaller upward, rarely reduced to thorns or scales, basal leaves when present often different and wider than those of the stem. *Inflorescence* mostly open-paniculate, occasionally racemose. *Heads* radiate, many flowered; involucral bracts in a few series, imbricate, mostly herbaceous at least near the tips, lanceolate or oblong with hyaline or scarious margins and sometimes subulate tips; receptacle slightly convex, naked; ray florets uniseriate or occasionally biseriate, the corollas exceeding the style and pappus, never yellow, apically dentate or entire, the style branches linear with margins generally thickened or papillose; disc florets perfect, the corollas mostly yellowish with a campanulate, 5-dentate limb, the anthers basally obtuse with ovate or oblong terminal appendages, the style branches oblong to subulate, dorsally papillose-pilose. *Achenes* somewhat flattened with 2–5 conspicuous nerves, glabrous or variously pubescent; the pappus in 1 or, less often, 2 series of fine, strigulose, white or buff bristles.

The genus *Aster* may be recognized by its solitary radiate heads with manifest ligules, by the flattened, laterally nerved achenes, and by the strigulose pappus. It is distinct from other genera in the usually broadened tips of the herbaceous portion of the involucral bracts. The sole Panamanian species is distinct from other members of the genus in its striking vegetative morphology, and it may warrant separation from *Aster*. At the same time, the structure of the involucral bracts and absence of pubescence argue against recognizing it as a member of the segregate genus *Leucosyris*.

When considered in the broad sense, this genus comprises 300 to 500 widely dissimilar species. Many workers consider that *Aster* will eventually be broken into many taxonomically acceptable segregate genera, but an overall consideration of the group is preferable to piecemeal fragmentation into heterodox units. In its full array the genus is nearly cosmopolitan in distribution with the greatest number of species in temperate regions. The type species is from southern Europe.

1. **Aster spinosus** Benth., Pl. Hartw. 20. 1839. TYPE: Mexico, *Hartweg 148* (K, not seen).—FIG. 35.

Leucosyris spinosa (Benth.) E. L. Greene, Pittonia 3: 244. 1897.

Erect wirey *herb* to 70 cm tall, woody at the base and spreading by rhizomes; stems green, drying with prominent angles, essentially leafless and bearing stout green spines. *Leaves* except those of seedlings and turoins reduced to linear scales to 10 mm long, or wanting. *Inflorescence* of numerous heads at the tips of slender

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[11] Many other names have been published which may be considered synonyms of *Aster*, depending upon the circumscription of the genus. *Leucosyris* is the only such name which applies to Panamanian material.

branches. *Heads* radiate; involucral bracts imbricate in few series, oblong, 5–7 mm long and 1–1.5 mm wide with a broad herbaceous midvein expanding slightly at the tip, the margin slender, hyaline, erose at the rounded apex; receptacle slightly convex, weakly alveolate, 1.5–2 mm across; ray florets in 1 series, the corollas white, ca. 5 mm long, the ligule oblanceolate and apically notched or entire, ca. 0.6 mm wide, the tube ca. 2.5 mm long, the style branches ca. 1 mm long, linear but somewhat flattened with thickened, papillose margins; disc florets perfect, 9 mm long, the corolla yellow, 5 mm long, the tube sparingly pubescent, the anthers 1.25 mm long, slightly exserted, obtuse at the base, the apical appendage obtuse, style branches exserted, resembling those of the ray florets but broader and more conspicuously papillose on the dorsal surface. *Achene* smooth, glabrous, flattened, with three prominent rounded angles, 1.2 mm long; carpopodium small and irregular in outline; pappus buff colored, uniseriate, strigulose, slightly exceeding the lobes of the disc florets.

This species is distinctive in its wiry, spiny stems which lack normal leaves. The numerous heads have white rays and yellow discs. It is a native of Texas and Mexico where it forms masses in ditches and other underdrained sites, spreading by underground rhizomes. In Panama it is known only from one collection. "Mexican devil-weed."

CHIRIQUÍ: Valley of the upper Río Chiriquí Viejo, *White & White 108* (MO).

35. BACCHARIS

Baccharis[12] L., Gen. Pl., ed. 5. 370. 1754. TYPE: *B. halimifolia* L.

Dioecious *trees* or *shrubs*, rarely *herbs*, erect or sometimes scandent or decumbent, mostly glabrate and often resinous. *Leaves* alternate (in Panama), simple, coriaceous or subcoriaceous, the venation pinnate, digitate or with few parallel nerves running to the apex, in some species reduced to thorns or scales or wanting and the stems alate with leaflike, sometimes jointed tissue. *Inflorescences* mostly somewhat compacted panicles, rarely solitary, racemose or spicate, the pistillate inflorescence usually larger than the staminate. *Heads* discoid with many florets, the pistillate heads larger than the staminate; involucral bracts imbricate in several unequal and often unlike series, indurate, the margin sometimes hyaline, apically erose, the midvein obsolete near the base; receptacle flat, convex or conical, mostly naked but in the pistillate heads sometimes paleaceous, usually muricate or verrucose, sometimes alveolate; pistillate florets slender to capillary, the corolla inflated at the base and tapering upwards, apically truncate, erose, or with a minute ligule, shorter than the involucre, the style well exserted, linear-oblong to linear, papillose-stigmatic, the ovary fertile; staminate florets tubular, the corolla clearly differentiated into a campanulate limb divided half-way or more into 5 lobes, the anthers basally obtuse or auricled, the appendages narrow, the style branches various but without manifest appendages, the ovary reduced or rudimentary, sterile. *Achene* cylindrical or somewhat compressed or angled;

[12] Several synonyms are listed by Cuatrecasas, Webbia 24: 234. 1969. Only the name *Baccharis* has been used for Panamanian material.

FIGURE 35. *Aster spinosus* Benth. Habit (× ½). [After *White & White 108* (MO).]

pappus of fine, often strigulose bristles in 1 or 2 series, sometimes twisted or crinkled and expanded at the apex, colored in some species, that of the fertile achene exceeding the involucre, that of the staminate (sterile) achene not exceeding the styles.

The genus *Baccharis* may be distinguished in Panama by its coriaceous leaves and often resinous twigs and foliage, by its essentially unisexual heads (an occasional floret of the opposite sex may be present), by the basal enlargement of the pistillate corolla, and by the deeply divided staminate corollas.

Baccharis is a large American genus with some 400 species most abundantly represented in South America. In Colombia 32 species are recognized (Cuatrecasas, 1969) while in Panama there are but two. *Baccharis* is thought to have evolved from *Conyza* or some other member of the Astereae by suppression of the bisexual character. When the genus is revised for South America as a whole, several distinct genera may be separated from the present circumscription of *Baccharis*.

Aristeguieta (1964) records that some species are useful in reforestation in Venezuela, and in Colombia some species are used on a local scale as dyestuffs. The foliage of some species is toxic to livestock, but the plant is unpalatable. In the Old World, particularly in India and Australia the Caribbean species, *B. halimifolia* L., has become naturalized as a noxious woody seed.

a. Plants glabrous except on emergent parts and petioles, young parts resinous; staminate involucral bracts more than 1.5 mm broad, the florets ca. 6 mm long, the limb lobed about halfway down, the sterile ovary longer than broad; pistillate receptacle with short to minute persistent paleas, usually blackening, the corollas inflated in the lower ⅓ portion ..... 1. *B. pedunculata*

aa. Plants minutely puberulent with fine, arachnoid hairs, mostly not resinous; staminate involucral bracts less than 1.2 mm broad, the florets ca. 4 mm long, the limb lobed nearly to the base, the sterile ovary disclike, shorter than broad; pistillate receptacle with elongate, deciduous paleas, not blackening, the corollas inflated in the lower ⅕ portion ..... 2. *B. trinervis*

1. **Baccharis pedunculata**[13] (Miller) Cabr., Bol. Soc. Argent. Bot. 7: 240. 1959.—Fig. 36A.

Conyza pedunculata Miller, Gard. Dict., ed. 8. 1768. TYPE: not seen.
Baccharis cinnamomifolia H.B.K., Nov. Gen. Sp. Pl. 4: 65. 1820 (1818). TYPE: *Humboldt & Bonpland* (P).
B. splendens Heering, Schriften Naturwiss. Vereins Schleswig-Holstein 13: 48. 1906. TYPE: not seen.

Glabrate *shrub* to 4 m tall; branches ascending, sometimes with conspicuous leaf scars, drying with many longitudinal striations and angles, often dark and somewhat reddish; emergent parts resinous. *Leaves* to 12 cm long, entire, elliptical, basally obtuse or acute, apically acute, acuminate or rounded and mucronate, beneath with 3(–7) prominent, elevated, stramineous, parallel nerves and finely reticulate, above with more or less obscure venation or a series of pinnate veins, glabrous, often resinous; petioles to 20 mm long, pubescent on the ventral surface, sometimes sharply angled. *Inflorescence* a corymb or panicle of many heads, to 15

[13] Other synonyms are listed by Cuatrecasas, Webbia 24: 269. 1969. Only the names listed have been used for Panamanian material.

Figure 36. *Baccharis*.—A. *B. pedunculata* (Miller) Cabr., Habit of female plant (× ½). [After *D'Arcy & D'Arcy 6360* (MO).]—B. *B. trinervis* Pers. Flowering branch (× ½). [After *D'Arcy 5217* (MO).]

cm long, overtopping the foliage; bracts small or scalelike; pedicels to 20 mm long, slender, drying strongly angled, ebracteolate. Pistillate *heads* discoid with campanulate involucres 4–5 mm long; involucral bracts loosely imbricate in several unequal series, the innermost narrowly oblong without distinct venation,

exceeding the pappus, the remainder obtuse or rounded with ciliate to erose margins, indurate, stramineous except for the short green midvein visible in the upper portion; receptacle 5–6 mm across, flat, muricate and short-paleaceous, becoming blackish; florets ca. 5 mm long, the corolla white, slender, tubular-corniculate, tapering from a broad base to the erose-margined apex, sparingly pubescent, the style exserted, its branches linear-obtuse, flattened, glandular papillose on the dorsal surface, the ovary glabrous except for a ring of short bristles near the base. Staminate *heads* discoid, smaller than the pistillate; receptacle flat, naked, often not blackening; florets 6 mm long, the corolla tube sparingly pubescent upwards, the limb ca. 2.5 mm long, lobed about halfway, the lobes acute or obtuse with thickened margins, the anthers 1.2 mm long, little exserted, basally slightly auricled, the appendages short-deltoid, the style densely glandular pilose upwards, its branches linear, papillose-pilose, the ovary (sterile) less than half as long as ovaries of the pistillate florets. *Achene* angled with a ring of short bristles at the base; pappus of fine, smooth or strigulose bristles in one series, buff colored.

This species is distinct by the black, flat disc with its short persistent paleas, and by the twigs and foliage being glabrate and resinous rather than puberulent.

Collections of *Baccharis pedunculata* from Panama have been taken in Coclé Province at middle elevations and from the Chiriquí mountains at middle and upper elevations. The species ranges from Costa Rica south and east to Peru and Venezuela.

CHIRIQUÍ: 1 mi S of Boquete, 4000 ft, *Allen 4721* (MO). Bajo Mono-Robalo Trail, Cerro Horqueta, 5000–7000 ft, *Allen 4827* (MO). Between Boquete and Monterey, *Croat 15807* (MO). Las Cumbres, 3040 ft, *D'Arcy 5305* (MO). Roadsides from Boquete to David above Río Cochea, *D'Arcy & D'Arcy 6304* (MO). Above Boquete on road to La Popa, 4800 ft, *D'Arcy & D'Arcy 6360* (MO). Boquete, *Davidson 643* (US). Volcán de Chiriquí, Boquete District, 7000 ft, *Davidson 890* (MO, US). Near Volcán, 4600 ft, *Duke 9146* (MO, US); *9170* (MO). Llanos Francia, 4000 ft, *Dwyer & Lallathin 8711* (MO, NY). Cuesta de Piedra (Cerro Punta), *King 5292* (US). 7 mi N of El Hato del Volcán, *King 5299* (US). Ca. 2 mi S of Boquete, *King 5316* (US). Near Boquete (to 3 mi N), 3300–4200 ft, *Lewis et al. 610* (MO, US). 4 mi from Boquete on road to David, *Kirkbride 91* (MO, NY). N of Dolega, *Partch 69–142* (MO). Pastures around Boquete, *Pittier 3125* (US). Palo Alto, 5000 ft, *Stern et al. 1049* (MO, US). Llanos Francia, 3300 ft, *Stern et al. 1182* (MO). 3 mi S of El Volcán, 4000 ft, *Tyson 875* (MO). Río Macho de Monte, 1 mi E of Cuesta de Piedra, 2800 ft, *Tyson 907* (MO). Bambito, 5600 ft, *Tyson 5657* (MO), *5868* (MO). Valley of upper Río Chiriquí Viejo, *White 238* (MO). Near Callejón Seco, Volcán de Chiriquí, 1700 m, *Woodson & Schery 491* (MO). Finca Lérida to Boquete, 1300–1700 m, *Woodson et al. 1101* (MO, NY), *1139* (MO, US, NY). COCLÉ: Near El Valle, 800 m, *Allen 784* (MO, US). Above El Valle 2 mi on road to La Mesa, *Croat 13316* (MO). Cerro Pilón near El Valle, 700–900 m, *Duke 12063* (MO). El Valle de Antón, foot of Cerro Pilón, 2000 ft, *Dwyer & Correa 7922* (MO). El Valle, *Ebinger 1104* (MO, US). Cerro Pilón, *Lallathin 5031* (MO). El Valle de Antón, 1000–2000 ft, *Lewis et al. 2505* (MO). N of El Valle de Antón ca. 7 mi, *Luteyn 1220* (MO). 2 mi S of El Valle, 600 m, *McDaniel 8244* (US). Llano Bonito N of Las Margaritas, 400–500 m, *Seibert 525* (MO, NY, US).

2. **Baccharis trinervis**[14] Pers., Syn. Pl. 2: 423. 1807.—FIG. 36B.

Weak *tree* or *shrub*, often somewhat scandent, to 4 m tall; branches arising at right angles, drying green with many longitudinal striations or angles, puberulent

[14] A number of synonyms are listed by Cuatrecasas, Webbia 24: 269. 1969. Only the above name has been used for Panamanian material.

with appressed arachnoid hairs, mostly not resinous. *Leaves* to 8 cm long, entire, elliptic, basally obtuse or acute, apically acuminate and sometimes mucronate, beneath with three prominent, elevated, parallel veins and finely reticulate, above with more or less obscure venation, puberulent to pilose on both sides, more so above, coriaceous; petioles to 15 mm long. *Inflorescence* paniculate, situated within or overtopping the foliage; peduncles stout, pubescent, to 20 cm long; bracts 20–25 mm long, leaflike, pilose; pedicels mostly less than 8 mm long, drying strongly angled with minute bracteoles on the lower half. Pistillate *heads* discoid, hemispherical or globose; involucral bracts imbricate in about 3 unequal series, the innermost acuminate, the remainder obtuse or rounded, apically erose, indurate, stramineous except for the short broad midvein visible in the upper portion; receptacle 1–2 mm across, conical, conspicuously muricate, with elongate, deciduous paleas 2–4 mm long; florets ca. 5 mm long, the corolla white, capillary, inflated near the base, apically erose, sparingly pubescent, the style long-exserted, its branches linear, flattened. Staminate *heads* discoid, smaller than the pistillate heads; involucral bracts dorsally puberulent; receptacle conical, naked, muricate, florets 4 mm long, the limb constituting more than half the corolla length, the tube divided nearly to the base into 5 lanceolate, apically acuminate, marginally thickened, glabrous lobes, the anthers ca. 1.3 mm long, fully exserted, basally auricled, the appendages narrow, the style pubescent upwards, its branches lanceolate, flattened, copiously glandular pubescent on the dorsal surface, the ovary (sterile) reduced to an inconspicuous disc between carpopodium and pappus. *Achene* densely pubescent; carpopodium prominent; pappus of fine strigulose bristles in 1 series, strigose and slightly larger near the apex, tawny or greenish colored.

This species is distinct in its puberulent vegetative parts, and in its elongate, deciduous paleas. The conical receptacle differs from the flat receptacle of the other Panamanian species. Pistillate and staminate plants differ not only in the sex of their flowers; the staminate plants also have narrower, less pubescent leaves and more pubescent involucral bracts.

Cuatrecasas (1969) recognized two varieties under *B. trinervis*. Variety *trinervis* has broader leaves and is less pubescent than var. *rhexioides* (H.B.K.) Baker. Both varieties may be identified in Panamanian material.

Baccharis trinervis ranges from Mexico to Peru and northern Argentina but does not extend east to Venezuela. In Panama it is a frequent plant from lower to upper elevations in all provinces, occurring wherever natural or man-made disturbance has taken place. "Santa Maria."

CANAL ZONE: Victoria fill near Miraflores Locks, *Allen 1744* (MO, NY). Barro Colorado Island, *Croat 4206* (MO, NY), *6457*, *7221* (both MO). 1 mi N of Summit Gardens, *Croat 8885* (MO). Ca. 1 mi N of Gamboa Gate on Pipeline Road, *D'Arcy 5217* (MO). Pipeline Road within 5 mi of Gamboa Gate, *D'Arcy & D'Arcy 6015* (MO). Fort Sherman, *Duke 4350* (MO). Barro Colorado Island, *Ebinger 38* (MO). Chagres, *Fendler 156* (MO), *161* (MO, US). Gamboa, *Heriberto 54bis* (US). Chagres River 1 mi N of Gamboa, *Lazor 3500* (MO). Between Corozal and Ancón, *Pittier 2646* (NY). Ancón Hill, *Pittier* 3 March 1906 (US). Barro Colorado Island, *Shattuck 583* (MO). Balboa, *Standley 27002* (US). Near Summit, *Standley 29589* (US). Between France Field and Cattival, *Standley 30288* (US). Between Matías Hernández and Juan Díaz, *Standley 32041* (US). Barro Colorado Island, *Starry 264* (MO). Miraflores Locks area, *Tyson 1254* (MO). 10 mi N of Gamboa, *Tyson 6313* (MO). Barro

Colorado Island, *Woodworth & Vestal 437* (MO). CHIRIQUÍ: Trail from Paso Ancho to Monte Lirio, upper Río Chiriquí Viejo, 1500–2000 m, *Allen 1472* (MO, NY). 1 mi SW of Boquete, 4000 ft, *Allen 4720* (MO). Palo Santo, 3 mi N of Volcán, *Croat 13551* (MO). Roadside from Paso Canoas to Cañas Gordas, *Croat 22212* (MO). Ca. 17 mi from David on road to Boquete, *D'Arcy & D'Arcy 6305* (MO). Bajo Chorro, Boquete District, 6000 ft, *Davidson 366* (MO, US). Río Chiriquí Viejo, N of Volcán, *Duke 8995* (MO). Tolé, *Dwyer & Hayden 7767* (MO). Llanos Francia, *Dwyer 8715* (MO). Near Boquete, 3300–4200 ft, *Lewis et al. 620* (MO). Pastures around Boquete, *Pittier 2872* (NY). Llanos Francia, 3300 ft, *Stern et al. 1222* (MO). Llanos just S of Boquete, *Stern et al. 1953* (MO, US). Finca Lérida to Boquete, 1300–1700 m, *Woodson et al. 1113* (MO, NY). COCLÉ: Hills S of El Valle de Antón, 600–800 m, *Allen 2864* (MO, US). Near Sardinilla, ca. 7 mi E of cement plant, *Blum & Tyson 496* (MO). Ca. 1 mi E of Santa Clara Beach, *D'Arcy 4087* (MO, NY). Santa Clara Beach, *Croat 9591* (MO). Road to La Mesa 2 mi above El Valle, *Croat 13299* (MO). Hills above El Valle de Antón, *D'Arcy & D'Arcy 6767* (MO). Cerro Pilón near El Valle, *Duke 12074* (MO). El Valle, *Dwyer 1937* (MO). Above El Valle, *Gentry 5624* (MO). Near Salamania, 8 mi E of Transisthmian Hwy., ca. 100 m, *Gentry 6705* (MO). El Valle de Antón, 1000–2000 ft, *Lewis et al. 2518* (MO). Santa Rita Ridge, *Lewis et al. 5266* (MO). 5 mi N of El Valle, 2500 ft, *Tyson et al. 2438* (US). Near Penonomé, *Williams 206* (NY). DARIÉN: Isla Boca Grande, *Duke 8839n* (MO). HERRERA: Between Ocú & Chitré, *D'Arcy 4144* (MO). Between Las Minas & Pesé, 600 ft, *Duke 12336* (MO). S of Ocú 12.5 mi, 1200 ft, *Lewis et al. 1666* (MO, US). LOS SANTOS: Loma Prieta, 800–900 m, *Duke 11903* (MO). Pocrí, *Dwyer 1119* (NY). 17.8 mi S of Macaracas, 1100 ft, *Lewis et al. 1594* (MO, US). Loma Prieta, Cerro Grande, 2400–2800 ft, *Lewis et al. 2230* (MO). Isla de Coiba, *Mendez 137* (MO). Between Tonosí and Macaracas, *Oliver et al. 3573* (MO). 12 mi S of Macaracas, *Tyson et al. 2931* (MO). PANAMÁ: Cerro Jefe, 2700 ft, *Blum & Duke 2186* (MO). 10 km N of El Llano on road to Cartí, *Busey 915* (MO). Finca del Indio, Cerro Jefe, *D'Arcy 5232* (MO). Panamá Viejo, *Duke 5727* (MO). Near top of Cerro Campana, *Duke 5989* (MO). Cerro Jefe, *Duke 9422* (MO). Cerro Campana, *Duke 10723* (MO). Coronado Beach, *Duke 11799* (MO). Río Pacora below Río Corso, *Duke 12024* (MO). Cerro Campana, *Ebinger 361* (MO, US). Camino de las Sabanas, *Heriberto 282* (US). Cerro Campana, *Lazor 2217* (MO). Near Panamá, *Macbride 2615* (US). Bellevista, Panama City, *Macbride 2740* (MO, US). Cerro Campana, 2600 ft, *McDaniel 6921a* (MO). Between Matías Hernández & Juan Díaz, *Standley 32041* (US). Just S of La Capitano, *Tyson 6763* (MO). VERAGUAS: Hills W of Soná, 500 m, *Allen 1025* (MO, US). Ca. 29 mi W of Santiago, *King 5280, 5277* (both US). Isla de Coiba, *Mendez 137* (MO).

36. CONYZA

Conyza Less., Syn. Gen. Comp. 203. 1832, not L.; nom. cons. TYPE: *C. chilensis* Spreng.

Leptilon Raf., Amer. Monthly Mag. & Crit. Rev. 2: 268. 1818. TYPE: *Erigeron divaricatus* Michx.

Erigeron sect. *Caenotus* Nutt., Gen. N. Amer. Pl. 2: 148. 1818. LECTOTYPE: *E. canadensis* L.

Laennecia Cass., Dict. Sci. Nat. 25: 91. 1822. LECTOTYPE: *L. gnaphalioides* (Kunth) Cass. = *Conyza gnaphalioides* Kunth.

Caenotus (Nutt.) Raf., Fl. Tell. 2: 220. 1836. "*Coenotus*" auct., orth. mut., not Nutt.

Annual or perennial *herbs*, rarely shrubby, our species erect and not truly rosette forming. *Leaves* alternate, simple, entire to pinnatisect, pubescent or glabrous. *Inflorescence* mostly of many heads in an open or compact panicle or sometimes racemose or subspicate along the terminal portion of the main stem, rarely of few or solitary heads; leaves of the flowering portion often smaller and of different shape from those lower on the stem. *Heads* disciform; involucral bracts imbricate in 1–several series with a herbaceous midvein and a hyaline margin, this usually contracted before the apex; receptacle naked, flat to slightly convex, smooth or muricate, sometimes darkened; outer florets numerous in many series, the corolla apices denticulate or minutely ligulate, the style branches exserted, linear, glandular-verrucose; inner florets fewer than the outer florets,

narrowly tubular, differentiated about mid-length into a tube and limb, the limb tubular, apically 5-dentate, the anthers basally rounded or obtuse, the appendages narrowly lanceolate to subulate, the style branches flattened with a thickened margin, dorsally papillose, its appendages triangular. *Achenes* uniform, much compressed, the margins thickened by two nerves, glabrous to pubescent; pappus of fine strigulose bristles in one or more series, the inner bristles about the length of the inner florets, the outer bristles when present shorter than the achene itself.

Conyza is distinguished from *Erigeron* by its short or absent ligules. It is included in *Erigeron* by many botanists. The florets are usually white or yellowish but in some species may be brownish. The genus is primarily pantropical with about 60 species, but some species are native to the temperate zones, and a few tropical species are wide ranging into temperate areas. Many species are troublesome weeds of towns and cultivation. "Horseweeds."

Conservation of the name *Conyza* Less. (Astereae) with the type *C. chilensis* over *Conyza* L. (Inuleae) and its type *C. squarrosa* L. resulted in a major reconstruction; many Old World species of *Conyza* L. have been or must be transferred to other genera as they are not congeneric with *Conyza* Less.

Literature:

Marshall, J. B. & D. McClintock. 1972. *Conyza* in Britain. Watsonia 9: 201–202. 1972.

a. Inflorescence an open panicle; pedicels elongate and slender, glabrate to puberulent.
  b. Lower leaves mostly scabrous, the teeth when present obtuse or rounded apically; receptacle 4–6 mm across; outer floret with a distinct ligule ---------- 1. *C. apurensis*
  bb. Leaves not scabrous, the teeth when present with pointed tips; receptacle less than 3 mm across; outer floret with or without a ligule.
    c. Outer florets with a distinct but minute ligule 0.5 mm long; receptacle 1–1.5 mm across; upper leaves linear, glabrate ---------- 3. *C. canadensis*
    cc. Outer florets apically dentate without a distinct ligule; receptacle 2–2.5 mm across; upper leaves narrow but not linear, mostly pubescent ---------- 2. *C. bonariensis*
aa. Inflorescence compacted or crowded in clusters or spikelike racemes; pedicels short and stout, lanate or tomentose.
  d. Lower leaves small (to 3 cm) and divided nearly to the margin into 3–7 teeth; stems arachnoid to lanate with soft, wispy hairs; inner florets less than 5 mm long, tubiform with a deeply cleft limb; achene with an irregular ring of glands near the apex ---------- 5. *C. schiediana*
  dd. Lower leaves larger than 3 cm, toothed or crenate but not deeply divided; stems puberulent to tomentose with dense spreading hairs; inner florets more than 5 mm long, tubular, the lobes not twice as long as wide; achene without glands ---------- 4. *C. chilensis*

1. **Conyza apurensis**[15] H.B.K., Nov. Gen. Sp. Pl. 4: 73. 1820 [1818]. TYPE: Venezuela, *Humboldt & Bonpland* (P, not seen).—Fig. 37.

Erigeron spathulatum Vahl in West, Bidrag Ste. Croix 303. 1793. TYPE: St. Croix, *West* (C, not seen), not *Conyza spathulata* Hoenem. 1815.

Pubescent ephemeral *herbs*, mostly erect, often branched, to 1 m tall in lowland areas, smaller in uplands; stems pilose near the base with spreading whitish hairs.

[15] Other synonyms are listed by Cuatrecasas, Webbia 24: 222. 1969. Only the names listed have been used for Panamanian material.

Lower *leaves* to 12 cm long, thin, spatulate; blade orbicular or elliptic, crenate toothed in the upper half, cuneate toward the base; petiole slender and narrowly winged, sparingly to densely pilose on both sides, the midvein prominent, the minor (pinnate) venation often obscure, upper leaves becoming smaller, entire, oblanceolate, sessile. *Inflorescence* an open panicle of many heads; pedicels to 20 mm long. *Heads* disciform, with many florets; involucral bracts imbricate, nearly equal, 3–4 mm long, the midvein flanked by stramineous, somewhat indurate tissue and a hyaline margin, sparingly pilose with long weak hairs; receptacle slightly convex, to 4 mm across, manifestly muricate and sometimes drying blackish; outer florets numerous in about 2 series, white, filiform with a distinct, minute, apically notched ligule to 1 mm long, rarely equalling or barely exceeding the pappus, the tube pubescent in the upper half, the style long-exserted, its branches short, linear-lanceolate, basally flattened; inner florets 3–5 mm long, the limb not much enlarged from the tube, apically 5-lobed, the anthers ca. 0.5 mm long, basally obtuse, apically with narrowly deltoid appendages, the style branches flattened, papillose-verrucose on the sides, glandular pilose on the short terminal appendages. *Achene* compressed, the margins somewhat thickened by two prominent veins, copiously pubescent; pappus of fine strigulose bristles in 1 series about as long as the inner florets.

This species is usually recognizable by the spathulate, crenate leaves near the base of the stem and by the numerous white florets. The large, muricate, often dark receptacle is also distinctive. The basal leaves are not scabrid as are those of *C. chilensis*. Lowland plants of *C. apurensis* are reminiscent of plants of *Erigeron annuum*, but that species has long, showy ligules and is not known to occur in lowland Panama.

Conyza apurensis ranges widely through tropical America. According to Cuatrecasas (1969) it is a native of Asia. In Panama it occurs at all elevations, but plants of the lowlands are much larger and coarser than those of middle and higher elevations.

CANAL ZONE: Barro Colorado Island, *Croat 5597, 8676* (both MO). Summit Garden, *Croat 15009* (MO). Old road to Gamboa between Madden Wye and Summit Naval Radio Station, *Croat 15022* (MO). Chagres, *Fendler 162* (MO). Barro Colorado Island, *Foster 970* (DUKE). Cerro Galera ca. 2 km from Pacific Ocean near W boundary of Canal Zone, *Gentry 6655* (MO). Fort Amador causeway island, *Tyson 5416* (MO). Macapale Island in Madden Lake, *Tyson 5487* (MO). CHIRIQUÍ: Quebrada Manzanillo, 9 km SSW of Puerto Armuelles, *Busey 722* (MO). Near El Hato del Volcán, *Croat 10710* (MO). Boquete Lookout, 4000 ft, *D'Arcy & D'Arcy 6327* (MO). Hwy. N of Cerro Panda, 6000 ft, *D'Arcy & D'Arcy 6619* (MO). Potrero, Boquete, 3800 ft, *Davidson 664* (MO). Near Boquete, 3300–4200 ft, *Lewis et al. 364* (MO). Near Boquete, 1200–1500 m, *Woodson & Schery 775* (MO). Finca Lérida to Boquete, 1300–1700 m, *Woodson et al. 1164* (MO). COCLÉ: La Mesa above El Valle, *Croat 14302* (MO). Above El Valle de Antón, *D'Arcy & D'Arcy 6737* (MO). Slopes of Cerro Pilón, 700–900 m, *Duke 12089* (MO). DARIÉN: Caná, 2000 ft, *Williams 724* (NY). LOS SANTOS: Loma Prieta, 800–900 m, *Duke 11873* (MO). PANAMÁ: Interamer. Hwy. near Tocumen Airport, *Croat 9768* (MO). Panama City on way to Tocumen, *D'Arcy & D'Arcy 6115* (MO). Between Cerro Azul and Cerro Jefe, *D'Arcy & D'Arcy 6228* (MO). Ca. 6 mi E of Chepo on Pan-Am. Hwy., *Duke 4064* (MO). Río Pacora just below Río Corso, *Duke 12030* (MO). Near Goofy Lake, *Lazor 5540* (MO). W slope of Cerro Campana, 2300 ft, *Tyson 4024* (MO). W slope of Cerro Campana, *Tyson 4025* (MO).

A
B

2. **Conyza bonariensis**[16] (L.) Cronq., Bull. Torrey Bot. Club 70: 632. 1943.

Erigeron bonariensis L., Sp. Pl. 863. 1753. TYPE: Herb. Linn. 994.11 (LINN, not seen).
Conyza floribunda H.B.K., Nov. Gen. Sp. Pl. 4: 69. 1820 (1818). TYPE: Quito, *Humboldt & Bonpland 3100* (P).

Coarse erect, sparingly branched ephemeral *herb* to 1.5 m tall; stems reaching 5 mm thick at the base, striate, green, evenly puberulent or sometimes glabrescent. Lower (few) *leaves* near the base broadly spatulate and dentate; median leaves to 10 mm long becoming somewhat smaller upwards, oblanceolate, entire or sparingly toothed, the base narrowed, sometimes into a petiolelike region, thin, puberulent, the midvein prominent, the minor venation obscure above, drying fine reticulate beneath. *Inflorescence* a many-headed open terminal panicle, much branched with scattered lanceolate bracts ca. 10–15 mm long; pedicels slender, to 20 mm long. *Heads* small, disciform with many florets; involucral bracts imbricate in ca. 2 series, 4–6 mm long, herbaceous with broad hyaline apically erose margins, glabrous to pilose; receptacle flat or slightly convex, 2–2.5 mm across, muricate; outer florets numerous, white, capillary, 3–4.5 mm long, apically denticulate, usually without a distinct ligule; inner florets few, yellow, clearly differentiated about halfway up into a slender, cylindrical limb, sparingly pubescent towards the top, the lobes deltoid-acuminate, glandular papillose at the tips, the anthers ca. 0.75 mm long, basally auriculate, apically with narrow appendages, the style branches broadly flattened with deltoid appendages, conspicuously glandular-pilose dorsally. *Achene* compressed, the margins slightly thickened by two prominent veins, pubescent, especially towards the base; pappus of fine strigulose bristles in 1 series, ca. 1.5 mm long.

The species is sometimes difficult to distinguish from *C. canadensis* or from large specimens of *C. apurensis*. In *C. canadensis* the leaves are narrower, the heads are smaller, the involucres and other green parts are generally less pubescent or glabrous, and there are small but distinct ligules on the outer florets. Large plants of *C. apurensis* which lack basal leaves may be distinguished by the large inner florets and by the manifest ligules on the outer florets.

Conyza bonariensis is nearly cosmopolitan in distribution, but Cuatrecasas (1969) indicates it may be a native of Argentina. In Panama it may be found in weedy areas throughout the country. Cuatrecasas distinguishes a puberulent var. *leiotheca* (Blake) Cuatr. with a glabrous involucre (most Panamanian plants) from the typical, densely pubescent var. *bonariensis*. Marshall & McClintock (1972) distinguished *C. bonariensis* from *C. floribunda*, but examination of type material revealed they are the same. They may be correct in recognizing two similar taxa in the British flora. "Tabaquillo."

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[16] Other synonyms are listed by Cuatrecasas, Webbia 24: 222. 1969. Only the names listed have been used for Panamanian material.

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FIGURE 37. *Conyza apurensis* H.B.K.—A. Lowland plant (× 3/10). [After *Croat* 5597 (MO).]—B. Upland plant (× 3/10). [After *Davidson 664* (MO).]

BOCAS DEL TORO: N slope of Cerro Horqueta, 6000–7000 ft, *Allen 5007* (MO). Without definite locality, *Wedel 324* (MO). CANAL ZONE: Barro Colorado Island, *Bailey & Bailey 363* (BH). Gaillard Hwy. near Paraíso, *Croat 10138* (MO). Gaillard Hwy. near Gamboa Bridge, *Croat 14899* (MO). Llanos Francia, 400 ft, *Dwyer & Lallathin 8722* (MO). Ca. 1 mi S of Madden Dam, *King 5238* (US). 1 mi NW of Gamboa, *Lazor 2247* (MO). Ancón Hill, *Standley 26315* (US). Sosa Hill, *Standley 26427* (US). Frijoles, *Standley 27622* (US). Río Pedro Miguel near East Paraíso, *Standley 30019* (US). Between France Field & Cativa1, *Standley 30364* (US). Near Fort Sherman, *Standley 31223* (US). Obispo, *Standley 31748* (US). CHIRIQUÍ: Near New Switzerland, 1800–2000 m, *Allen 1372* (MO). Escuela San Benito, Volcán, *Croat 10417* (MO). Monte Rey above Boquete, *Croat & Porter 15661* (MO); *Croat 15764* (MO). NW side of Cerro Panda, *Croat 15951* (MO). Between Cerro Punta and Bajo Grande, *Croat & Porter 15995* (MO). Quebrada Quanabanito beyond La Repressa, 2 mi SW of Puerto Armuelles, 0–200 m, *Croat 22040, 22073* (both MO). Near Las Nubes, 2.7 mi NW of Río Chiriquí Viejo W of Cerro Punta, 2200 m, *Croat 22360* (MO). First big bridge N of David on way to Boquete, ca. 800 ft, *D'Arcy & D'Arcy 6289* (MO). Slope of La Popa above Boquete, 5400 ft, *D'Arcy & D'Arcy 6414* (MO). Slope of Cerro Respinga above Cerro Punta, 8400 ft, *D'Arcy & D'Arcy 6567* (MO). Bajo Chorro, Boquete District, *Davidson 149* (MO, US). Llanos Francia, 400 ft, *Dwyer & Lallathin 8722* (MO). San Bartolo Limite, 12 mi W of Puerto Armuelles, 400–500 m, *Liesner 214* (MO). E of Boquete, *Stern et al. 1009* (MO). Bambito, 1 mi SW of Cerro Punta, 5600 ft, *Tyson 6521* (MO). COCLÉ: Cerro Pilón, *Lallathin* (MO). DARIÉN: Without definite locality, *Bristan 187* (MO). Near Campamento Buena Vista, Río Chucunaque above Río Tuquesa, *Stern et al. 874* (MO). LOS SANTOS: 5 mi S of Pocrí, *Croat 9730A* (MO). Los Toretos, *Dwyer 2436* (MO). 17.8 mi S of Macaracas, 1100 ft, *Lewis et al. 1618* (MO). PANAMÁ: Pan-Am. Hwy. near Jenine, Río Cañita, *Duke 3826, 3885, 3894* (all MO). 5–6 mi E of Chepo, *Duke 4026* (MO). Panamá Viejo, *Dwyer 2890* (MO). Juan Díaz, *Standley 30569* (US). Río Tapia, *Standley 28162* (US). Cerro Jefe, *Tyson et al. 4311* (MO).

3. **Conyza canadensis**[17] (L.) Cronq., Bull. Torrey Bot. Club 70: 632. 1943.

Erigeron canadensis L., Sp. Pl. 863. 1753. TYPE: Herb. Linn. 994.10 (LINN, not seen).

Coarse erect, sparingly branched ephemeral *herb to* 1.5 m tall; stems striate, glabrous to puberulent. *Leaves* to 10 cm long, linear or linear-lanceolate, sessile, entire or sparingly toothed, apically acute or acuminate, membranaceous, glabrous or sparingly pubescent on both sides, the midvein prominent and the minor venation obscure. *Inflorescence* a many-flowered open terminal panicle, much branched; bracts scattered, rarely to 15 mm long; pedicels slender, to 10 mm long. *Heads* small, disciform with many florets; involucral bracts imbricate in 2–3 unequal series, 3–4.5 mm long, mostly thin and glabrous; receptacle flat or slightly convex, 1–1.5 mm across, muricate; outer florets numerous, white, capillary, 2.5–3 mm long with a definite, short (0.7 mm) ligule; inner florets few, corolla, yellowish; slender, clearly differentiated about halfway up into a slender, cylindrical limb, sparingly pubescent or glabrous, the lobes deltoid-acuminate, the anthers ca. 0.5 mm long, basally obtuse and with obtuse appendages, the style branches flattened with short-deltoid appendages, thickened at the margins, glandular-verrucose dorsally and glandular pilose at the junction of branch and appendage. *Achene* compressed, the margins slightly thickened by two prominent veins, glabrous or pubescent, especially near base and apex; pappus of fine strigulose bristles in 1 series reaching or somewhat exceeding the inner florets.

This species is sometimes difficult to distinguish from *C. bonariensis*. It is distinct in its smaller heads, more glabrate, linear foliage, glabrous or glabrate

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[17] Other synonyms are listed by Cuatrecasas, Webbia 24: 222. 1969. Only the names listed have been used for Panamanian material.

involucral bracts, and in the presence of a definite, if small, ligule on the outer florets.

Plants smaller than usual with purplish-tipped involucral bracts have been recognized as var. *pusillus* (Nutt.) Cronq. This variety is common in the southeastern United States and includes the majority of Panamanian specimens of *C. canadensis*.

Conyza canadensis is nearly cosmopolitan in distribution but is perhaps more plentiful in temperate regions. In Panama it is found in weedy areas in upland Chiriquí. Plants from Europe tend to have more prominently ciliate leaves. "Pascueta," "Orozuz" (Puerto Rico), "Horseweed."

CHIRIQUÍ: Escuela San Benito, Volcán, *Croat 10413* (MO). Near El Hato del Volcán, *Croat 10711* (MO). Near Methodist camp near Nueva Suissa, *Croat 13528* (MO). Between Boquete & Monte Rey, *Croat 15805* (MO). Boquete, *D'Arcy & D'Arcy 6348* (MO). Potrero, Boquete, 3800 ft, *Davidson 663* (MO, US). Valley of Río Chiriquí Viejo, N of El Hato de Volcán, 5200–5600 ft, *Duke 9038* (MO). Near Volcán, 4600 ft, *Duke 9136* (MO). Near Boquete, 3300–4200 ft, *Lewis et al. 583* (MO, US). Nueva California, W of Volcán, *Tyson 6674* (MO).

4. **Conyza chilensis** Spreng., Novi Prov. Hort. Acad. Hal. 14. 1818. TYPE: Chile, *Chamisso* (not seen).

C. myosotifolia H.B.K., Nov. Gen. Sp. Pl. 4: 69. 1820, fide Cuatrecasas, Webbia 24: 209. 1969.
Erigeron chilensis (Spreng.) G. Don in Loud., Hort. Brit. 343. 1830.
Conyza arabidifolia Remy in Gay, Fl. Chil. 4: 76. 1849. TYPE: Chile, *Gay* (NY ex P).
C. yungasensis Rusby, Mem. Torrey Bot. Club 3: 55. 1893. TYPE: Bolivia, *Bang 202* (MO).
C. catharinensis Cabr., Bol. Soc. Argent. Bot. 7: 191, *tab.* 3. 1959. TYPE: Brasil, *Smith & Klein 7487* (LP, not seen). Cabrera's plate shows a damaged plant of *C. chilensis*.

Coarse erect, little branched ephemeral or short-lived perennial *herb* to 60 cm tall; roots fibrous and sturdy; stems to 6 mm thick at the base, puberulent to tomentose with spreading hairs, scabrous in the lower portion. Basal and lower *leaves* obovate to oblanceolate, to 12(–20) cm long, the basal portion cuneate and somewhat clasping the stem, the apical portion coarsely crenate, scabrous on both sides with short, sharp, stout-based hairs, the midvein prominent, the upper leaves becoming fewer and smaller, oblanceolate, oblong to linear, sessile and somewhat clasping at the base, mostly entire, mucronulate. *Inflorescence* terminal with few or many florets in a compact panicle or corymb; bracts linear, to 9 mm, inconspicuous; pedicels short, stout, tomentose. *Heads* relatively large, disciform with many florets; involucral bracts imbricate in several unequal series, the longest 7–8 mm long, stiff, the grey-green midvein with a prominent median groove flanked by stramineous, indurate ribs and a narrow hyaline margin, apically narrowly acute, dorsally scabrous with copious stiff, straight, ascending or loosely spreading hairs; receptacle flat, 4–6 mm across, brownish, conspicuously muricate; outer florets numerous, the corolla white, capillary, 5–6 mm long and slightly exceeding the involucre, glabrous or sparingly pubescent, apically dentate, usually without a distinct ligule, the style branches glandular, linear but slightly flattened with a median dorsal groove; inner florets fewer, yellowish or brownish, 5–6 mm long and slightly exceeding the outer florets, slightly differentiated into

tube and limb about halfway up the corolla, the limb pubescent with long ascending hairs and the upper portion angled, the anthers ca. 1.5 mm long, basally obtuse, apically with narrow appendages; the style branches flattened with thickened and slightly inrolled margins, copiously glandular-pilose dorsally and on the short-deltoid appendages. *Achene* compressed, slightly thickened at the margins by two veins, pubescent, especially towards the base; pappus of fine strigulose bristles in 1 or 2 series, the inner series as long as the inner florets, slightly longer than the outer florets, the outer series when presnt of a few bristles much shorter than the achene.

This species is distinct from other Panamanian elements in its strict, erect habit, its strigose foliage and involucres, and in its large florets. As in *C. bonariensis*, the outer florets are apically dentate without distinct ligules.

Conyza chilensis has been collected in Panama only in the Chiriquí mountains. It is widespread in the uplands of tropical America, ranging from Mexico to Argentina and Venezuela.

CHIRIQUÍ: Potrero, Boquete, 3800 ft, *Davidson 648* (MO). SW slopes of mts. just E of Chicá, *King 5265A* (US). Near El Hato de Volcán, *King 5302* (US). Between Cerro Vaca and Hato del Horo, Chiriquí, 850–1100 m, *Pittier 5397* (US). Near Boquete, 1200–1500 m, *Woodson & Schery 778* (MO).

5. **Conyza schiediana** (Less.) Cronq., Bull. Torrey Bot. Club 70: 632. 1943.

Erigeron schiedianus Less., Linnaea 5: 145. 1830. TYPE: Mexico, *Schiede & Deppe* (not seen).
E. subspicatus Benth. in Örst., Vidensk. Meddel. Dansk. Naturhist. Foren. Kjøbenhavn 82. 1852. TYPE: Costa Rica, *Örsted* (C, not seen).

Erect or decumbent pubescent *herb* to 30 cm tall, unbranched or much branched from the base; stems slender, densely leafy, arachnoid to lanate with weak, fine white hairs, drying reddish brown. *Leaves* small, sessile, the lower leaves on the stem 15 mm long, upfolded from the midvein, pinnatipartite with 1–3 irregular ascending lobes on each side, the lobes callose-tipped, the upper leaves numerous, 15 mm long, linear oblong but flared or auricled at the clasping base, apically mucronate, arachnoid pubescent. *Inflorescence* with many heads subspicate along the upper half or ⅔ of the stem, the heads crowded in pairs or small groups. *Heads* disciform with many florets, hemispherical to globose; involucral bracts slightly imbricate in about 3 unequal series, the longest ca. 3 mm long, the midvein broad, herbaceous, pubescent, especially near the base, the hyaline margin erose-ciliate, narrower near the apex; receptacle not observed; outer florets numerous, pale blue or almost white, capillary, 3 mm long, the tube sparingly pubescent in the upper half with a distinct, flat but hardly expanded, apically notched ligule 0.5 mm long; inner florets ca. 4.5 mm long, tubiform, the limb basally pubescent, deeply 5-lobed, the margins of the lobes thickened, the anthers ca. 0.7 mm long, basally slightly auricled, the appendages narrow, the style branches flattened and expanded upwards, the lanceolate or narrowly deltoid appendages and the branches copiously papillose-pilose. *Achene* compressed, the margins not thickened, 0.8 mm long, finely appressed pubescent and with an irregular ring of short-stalked glands near the apex; pappus of fine strigulose bristles in 1 series, slightly exceeding the corollas.

This species differs from other Panamanian species in a number of respects. The small, divided leaves and dense, spikelike inflorescences are good general characters, while the expanded, deeply cut limbs of the inner florets and the unthickened margin of the achene are good technical characters. The irregular ring of glands around the top of the achene is also distinctive.

This species is known in Panama from only one collection.

CHIRIQUÍ: Cerro Pando, upper Río Chiriquí Viejo Valley, *White 49* (MO).

37. ERIGERON

Erigeron L., Gen. Pl., ed. 5. 956. 1754. TYPE: *E. uniflorus* L.

Annual or perennial pubescent *herbs*, erect or prostrate, sometimes caespitose, sometimes woody, some species with rhizomes. *Leaves* alternate, sometimes forming rosettes, simple, entire or variously divided, herbaceous, sessile but the lower portion of the leaf often narrowed into a petiolelike region. *Inflorescence* scapose, solitary, or variously paniculate or corymbose. *Heads* radiate or nearly disciform; involucre campanulate or hemispheric, the involucral bracts in about 2 mostly subequal series, somewhat imbricate, herbaceous with a hyaline margin, narrow and apically attenuate, acute or subulate; receptacle flat to slightly convex, naked, alveolate or smooth; ray florets numerous, usually in about 2 series, fertile, the ligule slender to linear, rarely broad, exceeding the style and pappus, apically denticulate or entire; disc florets numerous, the corolla yellowish with a campanulate to infundibuliform, sometimes only slightly expanded limb and 5 regular apical teeth, the anthers basally obtuse, rarely auriculate, the appendage obtuse, oblong or almost linear, the style branches more or less flattened, dorsally papillose-pilose or verrucose with margins thickened, its apical appendages triangular lanceolate to linear, the ovary fertile or a few in the center abortive. *Achene* compressed, ovoid or ellipsoid, glabrous or pubescent with two nerves thickening the margins and sometimes 2–3 additional less conspicuous nerves on the sides; pappus of 1 or 2 series, the inner of fine strigulose bristles, the outer of shorter bristles, scales or wanting.

Erigeron is distinguished from *Aster* by the absence of an apical expansion of the herbaceous nerve of the involucral bracts and from *Conyza* in having ligules longer than the pappus or disc florets. *Erigeron* and *Conyza* are combined by some workers. In general, species of *Erigeron* may be recognized by the many white or bluish (never yellow) slender ray and yellowish disc florets. The nearly similar involucral bracts are arranged in about two imbricate series.

The genus *Erigeron* includes about 200 species almost worldwide in distribution but with the greatest number of species in North America. "Fleabanes."

a. Large erect plants to 1 m tall; stem leaves more than 6 cm long; stems becoming 3 mm thick; pappus of the ray florets composed of both bristles and scales ..... 1. *E. annuus*

aa. Decumbent or scapose plants less than 30 cm tall; stem leaves less than 5 cm long; stems less than 2 mm thick; pappus of the ray florets composed only of bristles in 1 or 2 series.

b. Plants scapose; stem leaves less than 10 mm long; involucral bracts more than 4 mm long; pappus as long as the disc florets; disc florets more than 3 mm long ..... 2. *E. cuneifolius*

bb. Plants decumbent; stem leaves more than 10 mm long; involucral bracts less than 4 mm long; pappus exceeding the disc florets; disc florets less than 3 mm long ..... 3. *E. karvinskianus*

1. **Erigeron annuus** (L.) Pers., Syn. Pl. 2: 431. 1807.—FIG. 38A.

Aster annuus L., Sp. Pl. 875. 1753. TYPE: not seen.
A. stenactis Krause in Sturm, Deutschl. Fl., ed. 2, 13: 54. 1905. TYPE: not seen.

Erect short-lived perennial *herb* to 1 m tall with a sturdy fibrous root and a small ephemeral rosette; stems striate-angled, puberulent with ascending, sometimes long and spreading, stout-based hairs. Basal *leaves* spatulate, the basal ⅔ narrowed into a slender petiole, slightly expanded and clasping at the base, the blades dentate with callose-mucronate teeth, scabrous above with sharp ascending hairs, beneath with some long white stiff hairs; stem leaves sessile, glabrescent, longer towards the middle of the stem (to 9 cm long and 15 mm wide) becoming smaller, entire and lanceolate towards the apex, the midvein prominent and flanked by a pair of weaker veins and another pair close to the margin. *Inflorescence* an irregular corymb or panicle of few to many heads; peduncles variable in length, each with 1 or 2 scalelike bracts along their length. *Heads* radiate; involucral bracts in two similar series, slightly imbricated, 3–4 mm long and 0.6–0.8 mm wide, tapering to an acute or acuminate sometimes elongate point, chartaceous with a relatively broad hyaline margin, pilose with conspicuous, ?glandular, thin-walled, large-celled hairs; receptacle 2.5–3 mm across, convex, manifestly alveolate; ray florets numerous in about 2 series, the corollas white, 5–10 mm long and 0.7 mm broad, apically notched or entire, the tube ca. 1 mm long, pubescent with ascending hairs, the style branches ca. 0.25 mm long, flattened and narrowly elliptical; disc florets numerous, yellow, 2–2.5 mm long, the tube ca. 1 mm long, the limb only slightly expanded, tubular-campanulate, prominently angled, the upper half comprising 5 thick-margined deltoid teeth, the anthers 0.6–0.7 mm long, not exserted, the appendages narrow. *Achene* compressed with two veins thickening the margins, densely pubescent, stramineous or greenish; pappus in 2 series, the inner of fine strigulose bristles not exceeding the disc florets, the outer of short, united scales usually much shorter than the achene, the achenes of the ray florets with scales only and lacking bristles.

This species is distinct from other Panamanian species in its robust, coarse habit and in its showy, numerous white ligules. It is distinct from most species of *Erigeron* of other areas in its dimorphic achenes, those of the ray florets with a pappus of scales and those of the disc florets with both scales and bristles.

Erigeron annuus is native to southern Canada and the adjacent United States but is naturalized southward and in Europe. In Panama it is known in Chiriquí Province at upper elevations where it is a frequent weed of gardens, cafetales, and towns. "Daisy fleabane."

→

FIGURE 38. *Erigeron*.—A. *E. annuus* (L.) Pers. Habit (× ¼). [After *Tyson 5670* (MO).] —B. *E. karvinskianus* DC. Habit (× ½). [After *Stern et al. 1960* (MO).]

A
B

CHIRIQUÍ: Cerro Punta, *Godfrey 67327* (MO). 2.2 mi below Cerro Punta, ca. 6000 ft, *Luteyn 895* (MO). 6.7 mi W of Boquete, 8000 ft, *Luteyn 1506* (MO). Audubon Cabin, Nueva Suiza, *Partch 69–9* (MO). 2.5 mi S of Cerro Punta, 5500 ft, *Sawyer* 1 March 1967 (MO). Bambito, 1 mi SW of Cerro Punta, 5600 ft, *Tyson 5620* (MO). Ca. halfway between Cerro Punta and Bambito, ca. 5600 ft, *Wilbur et al. 10950* (MO).

2. **Erigeron cuneifolius** DC., Prodr. 5: 288. 1836. TYPE: Puerto Rico, *Wydler 303* (not seen).

E. bellidioides Griseb., Cat. Pl. Cub. 149. 1866. TYPE: Cuba, *Wright* 2825 (not seen).

E. domingensis Urb., Symb. Antil. 3: 403. 1903. SYNTYPES: Hispaniola, *Eggers 2217, 2271* (not seen).

Diminutive rosette forming *herbs* developing a relatively stout rootstock. Basal *leaves* broadly obovate or spatulate to 3 cm long and 1.5 cm broad, the margins entire or with 2–5 teeth in the upper portion, glabrous to puberulent, more so beneath, minutely ciliate on the margins, the midvein strong and the minor venation more or less obscure. *Inflorescence* a scape to 30 cm tall, slender, puberulent with ascending hairs, the leaves scalelike to 10 mm long, lanceolate, basally partly clasping the stem and apically callose-glandular. *Heads* radiate, solitary or 1–3 near the top of the scape, ca. 4 mm high; involucral bracts imbricate in 2–3 unequal series, the longest ca. 3 mm long, narrowly lanceolate with a broad, erose hyaline margin, the herbaceous midvein extending into the tip; receptacle 1.5–3 mm across, convex, naked, alveolate; ray florets numerous in 1 or 2 series, 5 mm long, corollas white, the ligule 0.3 mm wide, the tube relatively long, 2–2.5 mm long, glabrous, the style branches linear, relatively short; disc florets 4 mm long, the corolla yellow, gradually expanding upwards with little distinction between limb and tube, anthers ca. 1 mm long, the appendages narrow, style branches flattened, copiously papillose-verrucose on the margin, the appendages half as broad as long. *Achene* much compressed with two veins thickening the margins, glabrous to densely pubescent; pappus of fine strigulose bristles in 1 series reaching the tips of the style branches, achene of the ray florets like that of the disc florets but narrower, perhaps not fertile.

This species is distinctive in its diminutive habit, spatulate to orbicular rosettes, and slender scapes with tiny leaves. The pubescence of the leaves, scapes, and achenes is quite variable.

Erigeron cuneifolius is known from only one Panamanian collection. It is plentiful in the Greater Antilles from where it was first described. Its range in Central America is uncertain. It has been confused with *E. jamaicensis* L. which has larger heads, more teeth on the rosette leaves, and larger leaves on the scape. *Erigeron cuneifolius* would seem to be closely related to *E. karvinskianus*. Portions of the above description (not of the heads) made use of Jamaican material.

CHIRIQUÍ: Savannas, Boquete, 3800 ft., *Davidson 730* (MO).

3. **Erigeron karvinskianus** DC., Prodr. 5: 285. 1836. TYPE: Mexico, *Karwinski* (M, not seen).—FIG. 38B.

E. mucronatum DC., Prodr. 5: 285. 1836. TYPE: Mexico, *Karswinski* (M, holotype, not seen; IDC 846 III 6, herb. DC.).

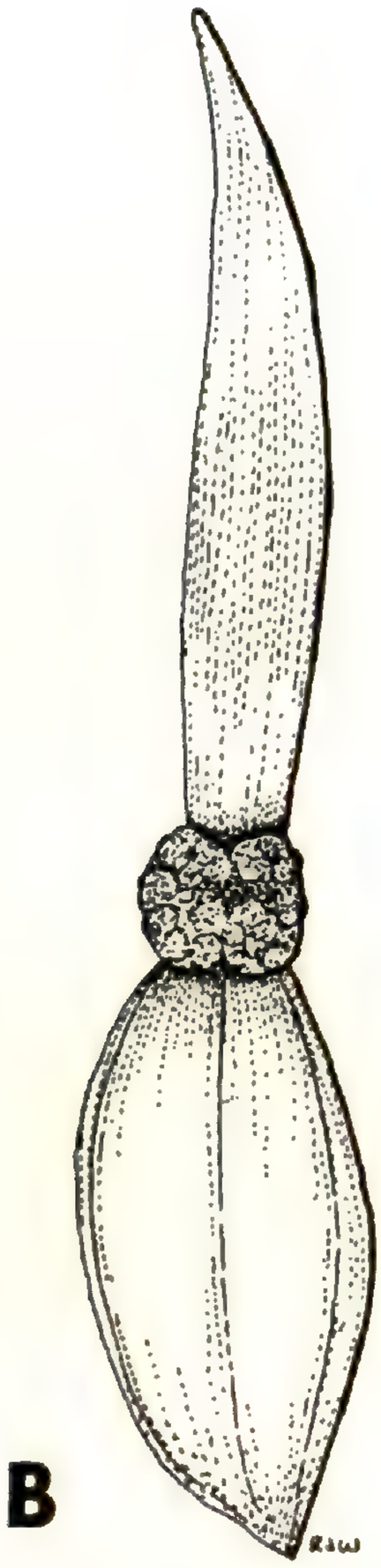
E. gaudichaudii DC., Prodr. 7: 274. 1838. TYPE: Peru, *Gaudichaud* (not seen).
E. karvinskianum var. *mucronatum* (DC.) Hieron., Bot. Jahrb. Syst. 28: 585. 1901. TYPE: not seen.
E. irazuense Greenman, Proc. Amer. Acad. Arts 40: 36. 1904. TYPE: Costa Rica, *Pittier 14075* (GH).
E. dissectus Urb., Symb. Antil. 7: 426. 1912. TYPE: Hispaniola, *Tuerckheim 3061* (MO).
E. maxonii Blake, Contr. U. S. Natl. Herb. 22: 594. 1924. TYPE: Panama, *Maxon 5306* (US, NY).
E. chiriquensis Standley, Publ. Field Mus. Nat. Hist., Bot. Ser. 22: 126. 1940. TYPE: Panama, *Davidson 872* (MO).

Diminutive branched *subshrub*, sometimes decumbent; stems flexuous, glabrate to arachnoid with slender white hairs, in age corky with prominent leaf bases. *Leaves* often clustered on the stem, to 7 cm long, variable in shape, those near the inflorescences smaller and nearly entire, lower leaves spatulate to oblanceolate, entire or variously 3–7 dentate in the upper portion, the sinuses shallow or almost reaching the midvein, the teeth glandular-callose, the apices acute, obtuse or rounded, the midvein prominent, minor veins following the midvein and diverging abruptly to the teeth, thus appearing pinnate, both surfaces sparingly pilose. *Inflorescences* mostly solitary heads at the ends of flowering branches with reduced leaves or more commonly on axillary peduncles which extend above the foliage; peduncles usually with one or two variously reduced bracts. *Heads* radiate; involucral bracts imbricate in about 3 series of slightly different length, 4–9 mm long, narrowly lanceolate, sparingly pilose with an erose-ciliate, hyaline margin, the midvein narrowed into the subulate tip, the outermost bracts sometimes purplish, the tips of the innermost darkened or purplish; receptacle 1.5–4.5 mm across, slightly convex, smooth or alveolate; ray florets in about 2 series, 10 mm long, the corolla white, bluish or purplish, the ligules ca. 0.8 mm broad, entire or apically notched, the tube 3 mm long with a few scattered hairs, the style branches linear, 1 mm long; disc florets 5–10 mm long, the corolla drying yellowish, tubiform, the limb hardly distinct from the tube, anthers 1–1.5 mm long, the appendages subulate-acute, the style branches 0.75 mm long, flattened, oblong with deltoid appendages, manifestly different from those of the ray florets. *Achene* flattened, the margins thickened by two conspicuous veins, copiously pubescent; pappus of fine, strigulose bristles slightly exceeding the disc florets and with at least a partial outer series of short bristles.

This species is quite variable in the size and color of the florets and in the shape of the leaves, but usually at least some leaves are dentate or lobed. In Panama it is distinct in its diminutive woody aspect, mostly solitary pedicels, and in the indistinct merging of the tube into the limb of the disc florets.

Erigeron karvinskianus is native to the upper elevations of tropical America. It ranges from Chile and Venezuela to Mexico and the Antilles. The species is also naturalized in the Old World and material has been seen from Ceylon, the Phillipines, and Tanzania.

CHIRIQUÍ: Summit and SW face of Cerro Copete, 9000 ft, *Allen 4884* (MO). Boquete District, 3800 ft, *Davidson 647* (MO, US). Potrero Muleto, Volcán de Chiriquí, Boquete District, 10400 ft, *Davidson 872* (MO, US), *1037* (MO). Cuesta Grande, E slope of Chiriquí mts., 2600–2900 m, *Maxon 5306* (NY, US). Finca Collins, El Velo, near Boquete, 6150 ft, *Stern et al. 1960* (MO). W slope of El Barú, 10000–11000 ft, *Tyson & Loftin 6144* (MO, SCZ). Chiriquí Viejo Valley, *White 101* (MO, US). Casita Alta to Cerro Copete, 2300–3300 m,



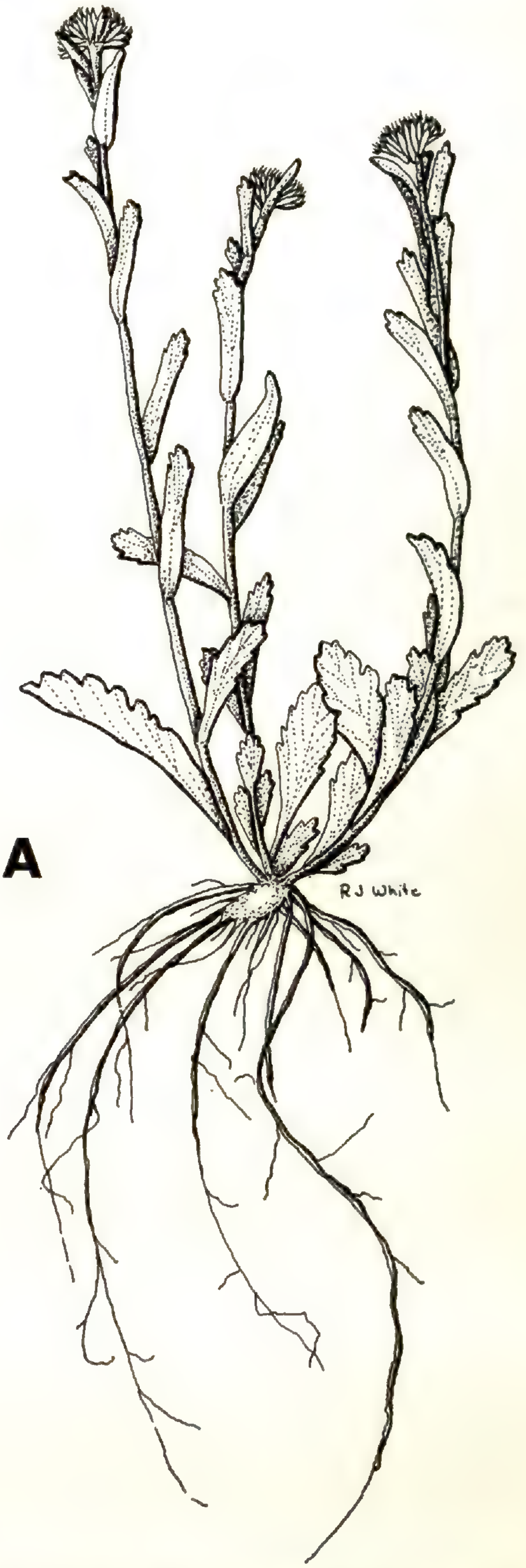


FIGURE 39. *Lagenifera panamensis* Blake.—A. Habit (× 3/5).—B. Achene with corolla (× 10 7/10). [After *Woodson et al. 1047* (MO).]

Woodson & Schery 363 (MO). Potrero Muleto to summit, Volcán de Chiriquí, 3500–4000 m, *Woodson & Schery* 397 (MO). Near Boquete, 1200–1500 m, *Woodson & Schery 776* (MO). Loma Larga to summit, Volcán de Chiriquí, 2500–3380 m, *Woodson et al. 1051, 1069* (both MO, NY).

38. LAGENIFERA

Lagenifera Cass., Bull. Soc. Philom. Paris, sèr. 3, 1815: 199. 1815. LECTOTYPE: *Calendula magellanica* Willd. = *Lagenifera nodicaulis* (Lam.) Dusén.

Lagenophora Cass., Bull. Soc. Philom. Paris, sèr. 3, 1818: 34. 1818, *Lagenifera*, orth. mut.

Scapose and caespitose *herbs*, some with a thickened rootstock or stoloniferous. *Leaves* forming rosettes, alternate and mostly petiolate and spatulate, the margins entire, sinuate or toothed, the teeth sometimes callose-tipped, pubescence of uniseriate, glandular or mostly eglandular hairs or wanting. *Inflorescence* a scape, slender or stout, leafy or leafless, or the few leaves reduced to scalelike bracts; peduncle not distinct from the scape. *Heads* solitary, manifestly radiate; involucral bracts numerous, imbricate, herbaceous with a single prominent midvein and inconspicuous hyaline margins, ciliate towards the apex; ray florets in 1–3 series, pink, purplish or white, the corollas ligulate or rarely tubular, the tube short and abscissing with a conspicuous callose or glandular ring at the base, the ovary laterally flattened with a prominent thickened margin, glabrous, obliquely turbinate with a narrowed stipelike base and a glandular peglike apex; disc florets clavate-crateriform corollas, the base of the tube like that of the ray floret, the anthers rounded or shortly auricled at the base with aristate appendages; the style branches usually more glandular and pubescent than those of the ray florets. *Achenes* shiny, flattened, the margin prominent, with a beak at each end, the apex sticky; carpopodium inconspicuous; pappus wanting.

The genus may be recognized by its scapose habit and by the laterally flattened achenes with their sticky apical beaks. As pointed out by Beaman & De Jong (1965), this genus is better placed in subtribe Grangeinae than in subtribe Bellidinae where it was placed by Hoffman (1894). The genus is perhaps most closely related to *Laestadia* Less. where there is also a narrow column with a glandular ring that separates the corolla limb and ovary body. *Laestadia*, which occurs in similar habitats from Bolivia to Costa Rica, has similar involucral bracts and scapelike inflorescences.

Lagenifera includes about 30 species distributed mainly on the periphery of the Pacific Ocean. *Lagenifera andina* Badillo (Venezuela), *L. cuchumatanica* Beaman & De Jong (Guatemala), and *L. maviensis* Mann (Hawaii) are all close relatives of *L. panamensis* and may in fact be extremes of one plastic species. This group is distinct from the species of Patagonia and the western Pacific in the stouter, leafy scapes, the dentate leaves, and the short style branches; it should probably be recognized as a separate subgenus.

Literature:

Beaman, J. H. & D. C. D. De Jong. 1965. A new species of *Lagenophora* (Compositae) from Guatemala. Rhodora 67: 36–41.

Cabrera, A. L. 1967. The genus *Lagenophora* (Compositae). Blumea 14: 285–308.

1. **Lagenifera panamensis** Blake in Woods. & Seib., Ann. Missouri Bot. Gard. 26: 314. 1939. TYPE: Panama, *Woodson et al. 1047* (US, holotype; MO, isotype).—FIG. 39.

Caespitose, scapose, perennial *herb* with a sturdy rootstock. Basal *leaves* spatulate to 5 cm long including the winged petiole, the blades ca. 2 cm long, elliptical, apically obtuse or rounded, the margin callose, dentate, glabrous but sparingly ciliate-margined with eglandular hairs, more so near the base, dried material with a scattering of whitish ?glandular spots visible with a lens on the upperside, the venation obscure above, beneath with about 3 ascending pinnate veins on each side of the midvein; leaves of the scape sessile and slightly clasping at the base, to 2.5 cm long and 3–5 mm broad, oblong, apically with 5–7 teeth much smaller than those of the basal leaves. *Inflorescence* a scape, 10–12 cm tall, evenly leafy to the summit and bearing a solitary head, glabrous or with a few scattered hairs along its length but pilose to arachnoid at the summit. *Heads* radiate, hemi-globose, 8–12 mm broad and ca. 6 mm tall; involucral bracts herbaceous, 1-nerved, oblong, 4 mm long and 0.6–0.8 mm wide, apically obtuse, glabrous but ciliate especially near the apex, purplish near the apex and with minute (?glandular) whitish spots; receptacle nearly flat, naked, ca. 8 mm wide; ray florets, ca. 57, 2-seriate, the corolla "pale pink-lavender," glabrous, 3 mm long, the tube short, basally thickened with a glandular-verrucose annulus which is hardly distinguishable from the apex of the ovary, the ligule lanceolate, its nerves obsolete and its margins slightly inrolled, the style branches 0.25–0.5 mm long, minutely papillose, the ovary laterally flattened, ca. 2 mm long, glabrous, obliquely turbinate, thick-margined, apically with a prominent peg-like, 0.25 mm long, glandular-verrucose beak and basally narrowing into a pseudostipe above the carpopodium; disc florets ca. 28, the corolla 2–2.5 mm long, the limb glabrous, campanulate, with 5 short teeth, the base of the corolla and ovary like those of the ray florets, the anthers 0.8 mm long, basally rounded or auricled, the appendage aristate, *Achene* shiny, compressed with prominent margins, the beak sticky, the base narrowed with an inconspicuous carpopodium; pappus wanting.

This species is known only from two collections. It may be recognized by the caespitose rosettes of dentate, spatulate leaves and by the small radiate heads. The glandular peg on the apex of the achene is distinctive in the Panamanian flora.

CHIRIQUÍ: Potrero Muleto, Boquete District, 10400 ft, *Davidson 1037* (US). Potrero, Loma Larga to summit of Volcán de Chiriquí, 2500–3380 m, *Woodson et al. 1047* (MO).

IV. INULEAE

W. G. D'Arcy[18]

Inuleae Cass., Jour. Phys. 88: 193. 1819. TYPE: *Inula* L.

Gnaphalieae Rydb., Fl. Rocky Mts. 833. 1917. TYPE: *Gnaphalium* L.

Herbs or *shrubs*, rarely *trees*; pubescence mostly arachnoid, stems sometimes glandular. *Leaves* alternate (Panama) or opposite, mostly cauline, mostly entire, often tomentose; petiolate or sessile. *Inflorescence* mostly paniculate or spiciform. *Heads* disciform, discoid, or seldom radiate; involucral bracts mostly numerous in several graded series, mostly indurate, overlapping, free, sometimes colored; receptacle flat or convex, mostly naked; ray florets with slender, mostly tubular corollas; disc florets with tubular-campanulate corollas; anthers connate, apically appendaged, basally obtuse, sagittate or tailed; style branches apically rounded or truncate, unappendaged; ovaries mostly terete. *Achene* mostly terete, small, often ribbed; pappus of numerous fine, strigose bristles.

This tribe may be recognized by the alternate leaves, arachnoid pubescence, and small, plump achenes. The Inuleae is especially well developed in the Old World and in Australia. Some species have in the past been confused with the Astereae but details of androecium and achene separate the two tribes in such cases of convergence.

a. Pappus bristles exceeding the involucral bracts.
  b. Involucral bracts, narrow, acicular, less than 1 mm wide; heads not pinkish.
    c. Stems conspicuously winged; leaves conspicuously different above and beneath; heads in a congested spikelike inflorescence; pedicels inconspicuous or wanting ..... 43. *Pterocaulon*
    cc. Stems not or only inconspicuously winged; leaves alike on both sides; heads in an open panicle; pedicels evident ..... 39. *Blumea*
  bb. Involucral bracts obtuse, often more than 1 mm broad; heads pinkish.
    d. Central, staminate floret solitary, the nectary larger than the achenes (Fig. 44); leaves becoming glandular punctate with a fine, dense, greyish tomentum on both sides ..... 44. *Tessaria*
    dd. Central, staminate florets 1–several, the nectary expanded but not as large as the achenes; leaves mostly not glandular punctate, the indumentum not dense above ..... 42. *Pluchea*
aa. Pappus bristles not exceeding the involucral bracts.
  e. Heads solitary, the pedicels evident; leaves not wooly, both sides alike.
    f. Involucral bracts green, acicular, less than 1 mm wide (native species) .... 39. *Blumea*
    ff. Involucral bracts mostly colored, acute or obtuse, more than 2 mm wide (cultivated species) ..... 41. *Helichrysum*
  ee. Heads glomerate, the pedicels occluded or wanting; leaves wooly beneath, the upper sides often glabrate ..... 40. *Gnaphalium*

39. BLUMEA

Blumea DC., Arch. Bot. (Paris) 2: 514. 1833, nom. cons. TYPE: *B. balsamifera* (L.) DC.

?*Laggera* Schultz-Bip. ex Benth. & Hook. f., Gen. Pl. 2. 290: 1873. TYPE: *L. purpurascens* Schultz-Bip. ex K.H.E. Koch.

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[18] Missouri Botanical Garden, 2315 Tower Grove Avenue, St. Louis, Missouri 63110.

Doellia Schultz-Bip. in Walp., Repert. Bot. Syst. 2: 953. 1843. TYPE: *D. kotschy* Schultz-Bip. (nom. nud.).
Placus Lour., Fl. Cochinch. 496. 1790. TYPE: *P. tomentosus* Lour. = *Blumea mollis* (D. Don) Merr.
Pseudoconyza Cuatr., Ciencia (Mexico) 21: 31. 1961. TYPE: *P. lyrata* (H.B.K.) Cuatr. = *Blumea viscosa* (Miller) Badillo.

Herbs or *shrubs*, annual or perennial, erect, ascending or sometimes procumbent; stems sometimes winged. *Leaves* alternate, simple, entire, or toothed, sometimes lobed, often glandular, pubescent; petiole wanting or short, sometimes winging the stem. *Inflorescence* solitary or paniculate, terminal or axillary, often aggregated into panicles, sessile or pedunculate, sometimes with paired bracts, bracteolate or not. *Heads* disciform, mostly small with many florets; involucral bracts numerous, imbricate in several series, dorsally pubescent, the margins scarious; receptacle flat or convex, naked or pilose; ray florets slender, the corolla mostly yellowish white, the style sometimes conspicuously exserted, the ovary fertile; disc florets fewer than the ray florets, the corolla apically (4–)5-lobed, the anthers with variously shaped apical appendages and slender tails, the ovary fertile or not. *Achenes* small, brown, oblong, 5–10-ribbed, plump, terete or obscurely 4-angled; pappus of numerous slender, strigose bristles in one series.

This genus may be recognized by its disciform, heterogamous heads, narrow, scarious-margined involucral bracts, naked receptacle, and mostly tailed anthers. The genus is, with the exception of the species treated here, entirely Old World in distribution. The American species has been placed in a number of genera but would seem most closely related to species such as *Blumea aurita* DC. and *Laggera kotschyi* Schultz-Bip. of Africa, and it is probably conspecific with some African species in this alliance. Randeria (1960) separated *Laggera* from *Blumea* because of its usually obtuse anther tips but Wild (1968) united the two genera. Superficially, *Blumea viscosa* treated here does not resemble the type species of either *Blumea* or *Laggera*, differing from *B. balsamifera* in having the pappus bristles in one rather than two series. If it is to be recognized as generically distinct, either the name *Pseudoconyza* or *Placus* should be used. The generic position of this species was further discussed by Badillo (1974).

Literature:

Badillo, V. M. 1974. *Blumea viscosa* y *Piptocarpha cuatrecasiana*, dos nuevas combinaciones en Compositae. Revista Fac. Agron. (Maracay) 7(3): 9–16.
McVaugh, R. 1972. Nomenclatural and taxonomic notes on Mexican Compositae. Rhodora 54: 495–516.
Randeria, A. J. 1960. The composite genus *Blumea*, a taxonomic revision. Blumea 10: 176–317.
Wild, H. 1968. The Compositae of the Flora Zambesiaca Area 2. Kirkia 7: 121–135.

1. **Blumea viscosa** (Miller) Badillo, Revista Fac. Agron. (Maracay) 7(3): 9. 1974.—FIG. 40.

Conyza viscosa Miller, Gard. Dict., ed. 8. 1768. TYPE: Veracruz, *Houston* (BM).
C. lyrata H.B.K., Nov. Gen. Sp. Pl. 4: 70. 1820. TYPE: Guayaquil, *Humboldt & Bonpland* (P).

Eschenbachia lyrata (H.B.K.) Britt & Millsp., Fl. Baham. 444. 1920.
Blumea lyrata (H.B.K.) Badillo, Bol. Soc. Venez. Ci. Nat. 10: 257. 1946.
Ernstia lyrata (H.B.K.) Pittier, Cat. Fl. Venez. 505. 1947, genus ined.
Pseudoconyza lyrata (H.B.K.) Cuatr., Ciencia (Mexico) 21: 31. 1961.
P. viscosa (Miller) D'Arcy, Phytologia 25: 281. 1973.
Blumea viscosa (Miller) D'Arcy, Phytologia 30: 5. 1975, redundant comb.

Herb to ?70 cm tall; stems solid or sometimes hollow, drying yellowish or greenish, striate, sparingly pubescent with long (1 mm) slender, simple hairs, and pulverulent-viscose with short and sessile glandular hairs, the glands often drying amber-colored. *Leaves* alternate, simple or basally divided into stipulelike auricles, obovate or spatulate, basally narrowed into a petiolelike region or not, the margins evenly dentate, the teeth mucronulate, the minor venation obscure, the midveins often prominent, both sides sparingly pilose with long slender simple hairs and short or sessile glandular trichomes. *Inflorescence* mostly an open panicle subtended by leaflike bracts; pedicels slender, to 12 mm long, sometimes much shorter or wanting, bracteolate or not. *Heads* cupular; involucral bracts many in several unequal series, the outer series herbaceous, lanceolate with strigulose margins and acute tips, strigose and glandular dorsally, the innermost slightly longer, more slender and more-or-less indurate, apically strigulose; receptacle naked, or with some small scattered simple hairs, mostly flat to depressed-hemispheric with a shallow central depression, 3–4 mm across; ray florets many, the corolla capillary, apically 3-notched, these in turn sometimes notched, ca. 3 mm long, little or not expanded basally, the style with a small nectary, the style branches mostly long exserted, the ovary fertile; disc florets few, 5 mm long, the corolla tubular, slightly expanded apically into a 5-toothed limb, slightly angled, the limb minutely pulverulent, the lobes with short, capitate hairs (colleters), the anthers ca. 1.2 mm long with fine basal tails and rounded, slightly longer than broad appendages, the style slightly expanded near the base, apically strigose and indistinct from the style branches which are unappendaged and open slightly or not at all, the ovary fertile. *Achene* brownish, plump, ellipsoid, prominently many-ribbed; pappus of numerous strigose bristles in one series.

Blumea viscosa occurs near seacoasts throughout the Caribbean region. Superficially much like species of *Conyza*, it differs in its dentate leaves which are much wider above the middle, in its plump achenes, and in the tails on the anthers. Several collectors report it to have a noxious odor. The species is closely related to African species such as *Blumea mollis* (D. Don) Merr. and species which Randeria (1960) placed in sect. *Paniculatae*. *Blumea viscosa* is the oldest name in the group.

McVaugh (1972) notes that there may be two distinct varieties in the species, and if this is the case, Panamanian material should be known as *Blumea viscosa* var. *lyrata* (H.B.K.) D'Arcy. The typical variety *viscosa* refers to pale-pilose plants, less glandular than those occurring in Panama. "Lechuguilla."

CANAL ZONE: Reserva forestal Madden, *Candido* 11 May 1970 (MO). Balboa, *Macbride & Featherstone* 37 (US). Ancón Hill, *Piper* 5572 (US). Balboa, *Standley* 30878 (US). COCLÉ: Aguadulce, *Pittier* 4966 (US). HERRERA: Las Salinas de Chitré on Bahia Parita E of Chitré,

FIGURE 40. *Blumea viscosa* (Miller) Badillo.—A. Habit (× ½).—B. Stamens (× 9⅗).—C. Achene (× 9⅗). [After *D'Arcy 4097* (MO).]

Croat 9691 (MO). LOS SANTOS: Between 1 mi S and 10 mi N of Tonosí, *Duke 12487* (MO). 5 mi S of Pocrí, *Croat 9738* (MO). PANAMÁ: Panama City, *Celestine 116* (US). Without definite location, *Duchaissing* (P). Isla Chepillo, *Duke 10328* (MO). Isla Espiritu Santo, *Duke 10450* (MO). Without definite locality, *Grisebach 1857* (MO). Las Sabanas, *Macbride 2671* (US). Saboga Island, *Miller 1977* (MO, US). Las Sabanas, *Standley 30692* (US).

40. GNAPHALIUM

Gnaphalium L., Sp. Pl. 850. 1753; Gen. Pl., ed. 5. 386. 1754. TYPE: *G. luteo-album* L. or *G. uliginosum* L.

Euchiton Cass. in Levr., Dict. Sci. Nat. 56: 215. 1828. TYPE: *E. pulchellus* Cass.
Omalotheca Cass. in Levr., Dict. Sci. Nat. 56: 218. 1828. TYPE: *O. supinum* (L.) Cass.
Gamochaeta Wedd., Chlor. And. 1: 151. 1855. TYPE: *G. americana* (Miller) Wedd.
Gnaphalion St.-Lag., Ann. Soc. Bot. Lyon 7: 127. 1880, nom. nud. TYPE: *G. dysodes* St.-Lag. (nomen).

Lanate or tomentose *herbs*, rarely suffruticose, often branched; stems leafy, rarely creeping. *Leaves* alternate, simple, entire or crenulate margined, lanate or tomentose at least in part, the hairs arachnoid, but sometimes glandular; petioles mostly wanting. *Inflorescence* an open or dense cymose panicle, racemose spike, or scapose with a congested, sometimes interrupted cluster of few or many heads, the clusters or heads mostly subtended by bracts or bracteoles. *Heads* small, disciform, with many florets, both staminate and pistillate florets present but often few of one sex, cyathiform or spindle shaped; involucral bracts many, imbricate in several series, sometimes apically corolloid, white, yellowish, sometimes with a rose or purplish cast; receptacle flat, naked, or sometimes with rudimentary, ephemeral chaff; ray florets with the capillary corolla basally expanded and contracted upwards, apically notched but without a distinct limb or ligule, the androecium wanting, the ovary fertile or rudimentary; disc florets tubiform, apically 5-lobed, about as long as the ray florets, the anthers connate, basally tailed, the tails sometimes fimbriate, the appendage obtuse, the style branches truncate, apically fringed with trichomes, unappendaged, the nectary conspicuous. *Achenes* little or not compressed, sometimes 4–many ribbed, glabrous or with glandular-appearing tubercles; pappus of fine smooth or strigulose bristles in one series, sometimes basally united and falling as a unit, in other cases free or nearly so and falling separately.

A genus of 100–300 species of cosmopolitan distribution, the species of *Gnaphalium* are most numerous in Africa, Mexico, and upland South America. A comprehensive revision of the genus has never been undertaken for any extensive region of the world, and a number of species have been named many times. The limits of the genus are not clear, and distinctions between *Gnaphalium* and *Anaphalis*, *Helichrysum*, and other groups may not be valid. Drury (1970) assessed a number of characters with a view toward delimiting these groups. Other discussions of these groups have been given by Cabrera (1961, 1963), Drury (1971, 1972), and Godfrey (1958).

Known in Panama as weeds of upland pastures and roadsides, many species in various parts of the world are credited with medicinal properties. Some are cultivated as ornamentals in temperate gardens. Although there are no reports of toxicity to livestock from living plants, some species may cause nitrate poisoning in stock when fermented with silage. "Cudweed," "Vira-vira" (Spanish).

Literature:

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Drury, D. G. 1970. A fresh approach to the classification of the genus *Gnaphalium* with particular reference to the species present in New Zealand (Inuleae-Compositae). New Zealand Jour. Bot. 8: 222–248.

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Godfrey, R. K. 1958. A synopsis of *Gnaphalium* (Compositae) in the southeastern United States. Quart. Jour. Florida Acad. Sci. 21: 177–184.

a. Inflorescence spicate; involucral bracts with brown tips; pappus united at the base and falling as a unit ——— 1. *G. americanum*

aa. Inflorescence of glomerules of heads, sometimes congested or in open panicles; involucral bracts without contrasting brown tips; pappus separating at the base and falling as separate bristles.

b. Leaves all lanceolate, not becoming linear near the inflorescence, glabrate and glandular above; receptacle 2–4 mm across; involucral bracts often chalky (under a lens) ——— 3. *G. domingense*

bb. Upper leaves mostly linear, especially near the inflorescence, eglandular, glabrate or pubescent above; receptacle less than 1.6 mm across; involucral bracts shiny, not chalky.

c. Heads often pinkish; inflorescence congested; leaves glabrescent above, those near the inflorescence often forming a pseudo-involucre; plants to 30 cm tall, branching at the base ——— 4. *G. roseum*

cc. Heads not pinkish; inflorescence often an open panicle; leaves mostly sparingly lanate above, not clustered near the inflorescence; plants to 70 cm tall, often branching above the base ——— 2. *G. attenuatum*

1. **Gnaphalium americanum** Miller, Gard. Dict., ed. 8. 1768. TYPE: not seen.

Gamochaeta americana (Miller) Wedd., Chlor. And. 1: 151. 1855.
Gnaphalium spicatum Lam., Encycl. Meth. 757. 1788. TYPE: Uruguay, Montevideo, *Commerson* (P).

Erect, ephemeral *herb*, sparingly branched; stems drying angled, silvery white with more or less appressed arachnoid hairs, to 50 cm tall. *Leaves* spatulate to oblanceolate, decurrent on the stem for a short distance but not auricled, mostly entire, apically mucronulate, strongly discolorous, the lower leaves dark above, to 5 cm long and 8 mm broad, sparingly arachnoid pubescent on emerging, soon glabrous, shiny, dark when old, beneath white-tomentose, the midvein prominent, the margins slightly revolute. *Inflorescence* an often-interrupted spicate raceme to 8 cm long and 15 mm thick, tapering upwards from below the middle, the heads in clusters of 1–6, the lowermost clusters subtended by leaflike, linear bracts which diminish upwards in the spike; pedicels lanate. *Heads* disciform cyathiform to fusiform, 3–5 mm high; involucral bracts imbricate in several series, the innermost equal, green-keeled with broad hyaline margins and the apical portion conspicuously dark brown, the outer series much shorter, broader, and lacking a conspicuous keel or brown tips; receptacle flat or slightly concave, naked, muricate; ray florets capillary, narrowed upwards, the corolla 1–2-notched and darkened, 3 mm long, numerous, the ovary fertile; disc florets few, 3 mm long, the corolla tubular, apically unequally 4-notched and darker, the tube white, the

anthers 4, with fimbriate basal tails, the appendages obtuse, the style branches truncate, apically glandular fringed. *Achenes* 1 mm long, fusiform, weakly 1–4-angled with sparse glandular trichomes or tubercules, weakly longitudinally muricate-striate, yellowish to amber colored, sometimes slightly compressed; pappus of many slender, 2–2.5 mm long, basally strigose bristles which may be acicular or expanded at the tips, basally connate and falling as a unit before the fruit is shed.

This species is recognizable by its spicate inflorescences, lanate pubescence on the leaf undersides, and the brownish tips of the inner involucral bracts. *Gnaphalium americanum* is a widespread weed of tropical and warm temperate regions, and it is plentiful in Panama in the Chiriquí mountains. Interpretation of the taxon bearing this name is based in part on the concept of Adams, Flowering Plants of Jamaica (1972). Both Drury (1971) and Godfrey (1958) distinguish between *G. americanum* and *G. spicatum*.

CHIRIQUÍ: Near New Switzerland, central valley of Río Chiriquí Viejo, 1800–2000 m, *Allen 1423* (MO). Trail N of Cerro Punta, *Croat 10486* (MO). N of Audubon Cabin, *Croat 13641* (MO—left and right specimens only). Between Boquete and Monte Rey, *Croat & Porter 15619* (MO). Monte Rey above Boquete, *Croat 15708* (MO). Boquete, *D'Arcy & D'Arcy 6351* (MO). Slope of La Popa above Boquete, 5400 ft, *D'Arcy & D'Arcy 6402* (MO). Bajo Chorro, Boquete District, 6000 ft, *Davidson 155* (GH, MO). Boquete, Finca Collins, 5000 ft, *Dwyer & Hayden 7682* (GH, MO). Fred Collins' Finca, *Ebinger 712* (MO). 0.5 mi S of Bambito, *Lazor & Correa 2704* (MO). From Boquete to 3 mi N, 3300–4200 ft, *Lewis et al. 424* (GH, MO). Alto Boquete, *Partch 69-82* (MO). Volcán de Chiriquí, 3500–4000 m, *Woodson & Schery 400* (GH, MO). Casita Alta, Volcán de Chiriquí, 1500–2000 m, *Woodson et al. 891* (MO).

2. **Gnaphalium attenuatum** DC., Prodr. 6: 228. 1838. TYPE: Mexico, *Berlandier 70* (P).

Erect, sparingly branched ephemeral *herb* to 70 cm tall; stems lanate with dirty white, arachnoid, appressed hairs, later glabrescent or floccose, striate when glabrous. *Leaves* linear-lanceolate to 6–11 cm long, 6(–10) mm wide, apically long acute or acuminate, basally contracted and slightly decurrent on the stem, the margins entire or nearly so, above glabrate but usually with wisps of arachnoid hairs, beneath lanate with dirty white hairs, and the midvein prominent or obscure, leaves smaller and linear near the inflorescence. *Inflorescence* a much or little branched, open panicle of clusters of flower heads; occasional linear bracts present. *Heads* disciform, 3–5 mm tall; involucral bracts imbricate, unequal, acute or obtuse, not chalky; receptacle 0.8–1.5 mm across, flat or slightly convex, muricate-punctate, often dark; ray florets many, ca. 3 mm long, the corolla capillary, slightly expanded at the nectary, apically 2–5-notched; disc florets several, ca. 3 mm long, the corolla tubiform, slightly expanded or bulbous at the nectary, the limb 5-lobed, glabrous, the anthers ca. 0.7 mm long, the basal tails fimbriate, the apical appendages narrowly deltoid, slightly longer than broad, the style branches equal, truncate and apically glandular-papillose, the nectary prominent, elevated above the top of the ovary. *Achene* reddish brown, 0.8 mm long, ellipsoidal, indistinctly 4–5-nerved and irregularly longitudinally striate; pappus basally strigose, bristles in one series about as long as the corolla, falling independently or in small weakly held groups.

This species is intermediate in some respects between *Gnaphalium domingense* and *G. roseum*. From *G. domingense* it differs in having conspicuously narrower leaves near the inflorescence and the leaf-uppersides mostly somewhat pubescent and eglandular. The involucral bracts also differ in not being chalky. From *G. roseum* it differs in its usually greater stature and more open inflorescence. The involucral bracts are not numerous near the inflorescence.

The name *G. attenuatum* is used here following a review of material annotated by Klatt in several herbaria.

CHIRIQUÍ: Summit and W face of Cerro Copete, 9000 ft, *Allen 4896* (MO). 20 km W of Puerto Armuelles, 400–600 m, *Busey 549* (MO). Trail N of Cerro Punta, *Croat 10529* (MO). Palo Santo, 3 mi N of Volcán, *Croat 13538* (MO). Above Cerro Punta on slope of Cerro Respinga, *D'Arcy & D'Arcy 6542* (MO). Lava fields near Volcán, 4600 ft, *Duke 9198* (MO). Along Boquete Trail, Cerro Respinga, 200–2500 m, *Gentry 5936* (MO). Mountains beyond La Pintada, 400–600 m, *Hunter & Allen 604* (MO). 6.7 mi W of Boquete, 8000 ft, *Luteyn 1496* (MO). Alto Boquete, 1125 m, *Partch 69-85* (MO). Cerro Pando, valley of upper Río Chiriquí Viejo, *White 12* (MO). Volcán de Chiriquí, 3500–4000 m, *Woodson & Schery 421* (GH, MO).

3. **Gnaphalium domingense** Lam., Encycl. Meth. 2: 743. 1788. TYPE: Hispaniola (not seen).

G. poeppigianum DC., Prodr. 6: 227. 1837. TYPE: Peru, *Poeppig 1368* (G-DC, not seen, IDC 1067. I, 1; W, isotype, not seen, MO, photo).
G. portoricense Urb., Symb. Ant. 3: 409. 1903. SYNTYPE: Puerto Rico, *Sintenis 205* (MO).
G. viscosa sensu auct., ?an H.B.K.

Herb to 2 m tall; stems lanate with a bright to dirty white tomentum of arachnoid hairs. *Leaves* lanceolate, to 10 cm long and 2 cm broad, becoming smaller near the inflorescence, apically acute, mucronulate, the margins entire or crenulate-undulate, above green, often with a few wisps of arachnoid hairs, especially near the base of the midvein, the venation obscure, drying dark with short, stout glandular trichomes, beneath lanate tomentose, the midvein prominent, basally somewhat auricled, slightly clasping the stem and sometimes appearing decurrent. *Inflorescence* an open cymose or round-topped panicle, the heads in glomerules of 1–5, subtended by small, narrowly lanceolate leaflike bracts. *Heads* disciform, 4–6 mm long; involucral bracts many, imbricate, unequal, mostly obtuse, the apices of the innermost with a chalky appearance when viewed under a lens; receptacle 2.5–3 mm across, flat or slightly convex; ray florets numerous, 4–5 mm long, the corolla capillary, with a bulbous basal enlargement around the nectary, basally glandular papillose, apically 4–5-notched, darker colored; disc florets 4–5 mm long, the corolla tubiform, with a bulbous basal enlargement around the nectary, basally glandular-papillose to puberulent, apically 5-lobed, the anthers 1.2 mm long, the tails fimbriate, the appendages twice as long as broad, rounded, the style with a conspicuous, stipitate nectary, the style branches variable, often unequal, apically truncate and weakly glandular fimbriate, sometimes flattened dorsiventrally and glandular on the adaxial surface. *Achene* reddish brown, ca. 1 mm long, wrinkled-striate, unnerved or weakly 3–5-nerved; carpopodium distinct, pale, oblique; pappus of many basally strigose and flattened bristles which fall independently or in small groups.

This species is distinct from other Panamanian species of the genus in its chalky involucral bracts, large receptacle, and broad leaves which lack tomentum on the ventral surface but bear short glandular trichomes. In Panama, *Gnaphalium domingense* is known only from the uplands of Chiriquí Province. It may hybridize with *G. attenuatum*, and it is sometimes difficult to separate the two species. *Gnaphalium domingense* ranges widely in the New World tropics where it is known by many names. No attempt is made here to provide more synonymy than is necessary for working with the Panamanian plants. Much Panamanian material has been known under the name *G. oxyphyllum* DC., a later name based on material from Mexico. *Gnaphalium domingense* differs from the similar *G. obtusifolium* L. of eastern North America in the glands and gland-tipped hairs on the upper surface of the leaves; leaves of *G. obtusifolium* are glabrous.

CHIRIQUÍ: Near New Switzerland, central valley of Río Chiriquí Viejo, 1800–2000 m, *Allen 1374* (MO). Cerro Punta, ca. 7000 ft, *Blum et al. 2417* (MO). Camino al Cerro de la Muerte, 6000 ft, *Correa 1267* (MO). Between Cerro Punta and Las Nubes, ca. 1800 m, *Croat 26386* (MO). 1.4 mi SW of Cerro Punta, *Graham 296* (GH). Bajo Chorro, Boquete District, 6000 ft, *Davidson 432* (GH, US). Ca. 7 mi from El Hato del Volcán, *King 5300* (US). Foot of Sierra Boquete, 4300 ft, *Maurice 900* (MO). Cerro Vaca, 900–1136 m, *Pittier 5309* (GH). 1 mi S of Cerro Punta, 6000 ft, *Tyson 5781* (MO). Near Callejón Seco, Volcán de Chiriquí, 1700 m, *Woodson & Schery 494* (MO). N of Audubon Cabin, *Croat 13641* (MO—middle specimen only).

4. **Gnaphalium roseum** H.B.K., Nov. Gen. Sp. Pl. 4: 81. 1820. TYPE: Colombia, Guananuato, *Humboldt & Bonplandt* (P).—FIG. 41.

Erect, apparently perennial *herb*, branched mostly at the base with a small but sturdy tap root, perhaps creeping by stolons; stems copiously leafy, tomentose with appressed greyish or yellowish white, lanate, arachnoid hairs. *Leaves* linear or linear-lanceolate, to 3 cm long and 3 mm wide, the margins entire or undulate, often with a crenulate appearance, above tomentose except on the emerging margins but soon glabrescent, mostly drying dark, beneath yellowish or greenish-tomentose except for the margins, the midvein occluded, apically long acute and mucronulate, basally slightly broadened and shortly decurrent on the stem. *Inflorescence* a congested, terminal panicle of short-stalked clusters, the subtending leaves often forming a partial involucre; pedicels short, tomentose. *Heads* disciform, 4–6 mm long; involucral bracts many in several unequal series, obtuse or acute, shiny, minutely and evenly striate, under a lens appearing glandular but not chalky, mostly stramineous but sometimes roseous due to the color of the glandular material; receptacle ca. 2 mm across, flat; ray florets many, the corollas capillary, ca. 3 mm long, bulbous near the base around the nectary, apically 5-lobed; disc florets several, the corollas tubular, basally bulbous around the nectary, apically 5-lobed, the anthers 1.5 mm long, basally fimbriate-tailed, the appendages twice as long as broad, obtuse-deltoid, the style with a prominent nectary situated above the base of the corolla, the style branches truncate, the apical margins glandular papillose. *Achene* (immature) reddish, 0.8 mm long; pappus of basally strigose bristles about as long as the corollas, falling separately.

This species may have yellowish, brownish, or pink to purplish heads, the color deriving from minute, gland-like thickenings of the end-walls of the elongate,

A
B
J.C. WILSON
JLW

evenly parallel cells of the tissue of the involucral bracts. These evenly disposed cells also give a finely striate, silky texture to the bracts which is wanting in other Panamanian species of the genus. The tomentum of the upper surface of the leaves is usually very early deciduous and the uppersides of the leaves then appear quite glabrous. In the type collection, both sides of the leaf are tomentose.

In Panama *Gnaphalium roseum* is known only from near the summit of Volcán Chiriquí, above 3000 m.

CHIRIQUÍ: Volcán de Chiriquí, 10400 ft, *Davidson 1039* (GH, MO, US). Peak, Volcán de Chiriquí, Boquete District, 11960 ft, *Terry 1323* (GH, MO). Volcán de Chiriquí, *Sapper* April 1899 (US). Top of El Barú, 11000 ft, *Tyson & Loftin 6179* (MO). Volcán de Chiriquí, 3500–4000 m, *Woodson & Schery 429* (MO). Volcán de Chiriquí, 2500–3380 m, *Woodson et al. 1054* (MO).

41. HELICHRYSUM

Helichrysum Miller, Gard. Dict., ed. 4, abr. 1754. "Elichrysum." TYPE: *H. orientale* (L.) Gaertn. Name and type conserved.

Herbs or rarely *shrubs*, mostly lanate or arachnoid-pubescent. *Leaves* alternate, entire or nearly so, mostly without a distinct petiole, mostly narrow. *Inflorescences* solitary, congested or in open panicles, mostly terminal on the stems, leaflike; bracts commonly present. *Heads* disciform or discoid with mostly or entirely hermaphrodite (disc) florets; involucre of many imbricate, persistent paleaceous bracts, mostly in indefinite series, sometimes brightly colored; receptacle mostly flat and naked; disc florets tubular, apically 5-lobed, the anthers with setose or capillary tails, sometimes branched or fimbriate, apically with elongate, obtuse appendages, the style branches slightly expanded and dorsiventrally flattened upwards, the nectary often prominent, apically pointed. *Achene* plump, often slightly curved or oblique, indistinctly nerved; pappus of many strigose bristles in one series.

A genus of several hundred species widely distributed in the Old World. The chaffy involucral bracts are persistent and give the heads a radiate appearance although true ray (ligulate) flowers are mostly inconspicuous or wanting. Several species are cultivated for ornament.

1. **Helichrysum bracteatum** (Vent.) Andrews, Bot. Rep. Sup. 1, *tab.* 428. 1805; Willd., Enum. Pl. Hort. Berol. 869. 1809.

Xeranthemum bracteatum Vent., Jard. Malm. *tab.* 2. 1803. TYPE: not seen.

Ephemeral *herb* to 1 m tall, glabrate or puberulent with short glandular hairs and sparse, arachnoid hairs; stems green, drying striate. *Leaves* alternate, sparsely pubescent with arachnoid hairs, entire, to 12 cm long, oblanceolate, the margin undulate, narrowed in the lower portion into a petiolelike region; petiole indistinct. *Inflorescence* of solitary heads terminating the uppermost branches;

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FIGURE 41. *Gnaphalium roseum* H.B.K.—A. Habit (× ⅗).—B. Achene (× 25). [After *Davidson 1039* (MO).]

several linear, leaflike bracts present under the heads. *Heads* showy, falsely radiate; involucral bracts many in several nearly equal series, the outermost obtuse, the innermost shorter and acute, paleaceous, persistent, 10–15 mm long, variously orange, yellow, purple, or white, the innermost usually lighter colored; receptacle flat, 15–25 mm across; ray florets few or wanting; disc florets 10 mm long, corolla tubular, sharply expanded basally at the nectary, broadened about ⅔ up, apically 5-lobed, the anthers 3 mm long, with separate, setose tails, the appendages acute, slightly more than twice as long as broad, the style branches apically deltoid, the upper half of the branch slightly expanded laterally, compressed dorsiventrally, papillose-glandular near the apex, the nectary prominent, indistinctly lobed, elevated above the top of the ovary by an obconical process. *Achene* plump, fusiform-reniform, dark colored, indistinctly nerved or striate, ca. 3 mm long; carpopodium indistinct, oblique, a persistent apical flange subtending the pappus; pappus of yellow or white strigose bristles in one series about as long as the corollas.

Cultivated in the Chiriquí region as an ornamental for sale as cut flowers in markets. "Everlasting," "Inmortal" (Spanish).

CHIRIQUÍ: Purchased in market, David, said to be grown at Volcán, *D'Arcy & D'Arcy 6285* (MO).

42. PLUCHEA

Pluchea[19] Cass., Bull. Sci. Soc. Philom. Paris 1817: 31. 1817. TYPE: *P. marylandica* (Michx.) Cass. = *P. odorata* (L.) Cass.

Herbs or *shrubs*, often aromatic, glabrous or pubescent, sometimes glandular; stems sometimes winged. *Leaves* alternate, simple, entire or toothed, mostly with a prominent midvein, sessile or petiolate, sometimes auricled or decurrent on the stem. *Inflorescences* few or many terminal panicles of congested heads, often round or flat tipped; bracts leaflike, scalelike, or wanting. *Heads* disciform with many florets, the involucral bracts imbricate in a few unequal series, ovate, obtuse, herbaceous to indurated, often with a scarious margin or ciliate, sometimes a few innermost acute, longer and paleaceous; receptacle flat, naked; ray florets numerous, the corolla slender or capillary, often purplish upwards, glabrous except on the lobes, apically 2–3-notched or toothed, basally expanded around the style base, the style branches mostly not exserted, the ovary fertile; disc florets few, the corolla tubular, campanulate, the tube slender, sometimes basally expanded, the limb with 5 deltoid lobes, the anthers 2 mm long, the appendages rounded, about twice as long as broad, the adjacent basal tails mostly united, the style branches mostly united, hirsute, flattened-fusiform, the style base expanded, the ovary rudimentary, sterile. *Achene* cylindrical, prominently 3–6-ribbed, strigose, often glandular; pappus of strigose, basally united bristles in one series.

Pluchea includes fewer than a dozen species, mainly of the Caribbean region and eastern North America. In Panama the genus is restricted to one cultivated

[19] For a list of generic synonyms see Godfrey (1962). Only the above name has been used for Panamanian material.

species and another species which occurs occasionally, probably as an adventive. The pale purplish or mauve flowers, the aromatic foliage, and the stramineous, pappuslike ribs on the cylindrical achenes are good features for recognition.

Literature:

Godfrey, R. K. 1962. *Pluchea*, section *Stylimnus*, in North America. Jour. Elisha Mitchell Sci. Soc. 68: 238–271, *pls.* 20–23.

a. Shrub, often over 1.5 m tall; leaves subentire, often more than 8 cm long with usually more than 7 veins on each side of the midvein; cultivated species ..... 1. *P. carolinensis*
aa. Herb, not exceeding 1.5 m tall; leaves mostly serrate-dentate, mostly less than 8 cm long with usually fewer than 7 veins on each side of the midvein; adventive species ..... 2. *P. odorata*

1. **Pluchea carolinensis** (Jacq.) G. Don in Sweet, Hort. Brit., ed. 3. 350. 1839.

Conyza carolinensis Jacq., Coll. 2: 271. 1788 (1789); Ic. Pl. Rar. 3, *tab.* 585. 1788 (1789).
TYPE: not seen.
C. odorata sensu Godfrey, Jour. Elisha Mitchell Sci. Soc. 68: 247. 1952, not L.

Branched *shrub* to 4(–5) m tall; twigs minutely whitish to reddish cinereus with fine, weak, spreading or crumpled hairs, drying faintly angled. *Leaves* elliptical to lanceolate, mostly to 10–12 cm long, 3–5 cm broad, apically acute or obtuse, mucronulate, basally acuminate or acute, the margins entire or with a few teeth, ca. 8 veins on each side of the prominent midvein, wider spaced upwards, felty tomentose beneath with weak whitish or greyish hairs, drying lighter beneath; petioles stout, 10–15 mm long, fine-tomentose. *Inflorescence* a somewhat congested cymose panicle with many florets, held erect above the foliage, with undifferentiated bracts and occasional linear bractlets ca. 5 mm long. *Heads* campanulate-cyathiform, somewhat flat-topped, disciform; involucral bracts numerous in several unequal series, indurated, dorsally tomentose, ca. 2 mm long, apically rounded to acute, entire, minutely erose or ciliate; ray florets numerous, capillary, 4 mm long, the corolla purplish, apically denticulate, basally expanded around the style base, the style branches slender, the style base globose, ca. 3 times the diameter of the style, elevated from the ovary on a distinct stipe, the ovary fertile, slightly flattened, oblong-cylindrical, basally expanded at the carpopodium and apically expanded at the pappus, the 3–5 ribs pubescent with ascending hairs; disc florets few, 5 mm long, the corolla narrowly tubular, expanding upwards, the 5 apical lobes dorsally papillose with whitish trichomes, otherwise glabrous, the anthers 2–3 mm long, the appendages narrowly obtuse, the basal tails filiform, partly connate, the style branches flattened, the style base expanded-globose, the ovary rudimentary, sterile. *Achene* reddish brown, ca. 1 mm long, cylindrical with pronounced stramineous ribs, the basal area and carpopodium yellowish; pappus of numerous barbellate bristles in one series, ca. 4 mm long.

This species is known in Panama only in cultivation. It is grown around homes and sold in markets as a medicinal. "Salvia," "Curforal."

Godfrey (1962) applied the name *Pluchea odorata* to this species. Lecto-

typification of *Conyza odorata* correctly reassigns that name to the other Panamanian species of *Pluchea* leaving *Pluchea carolinense* as the correct name for the taxon described above.

CANAL ZONE: Curundú at house no. 2114, tea used as cure for chest cold, *Tyson 3467* (MO). COLÓN: Sold in Colón market for "tea" by Jamaican weedwomen, *D'Arcy 3993* (MO). VERAGUAS: Semicultivated, Santa Fe, *Gentry 2945* (MO).

2. **Pluchea odorata** (L.) Cass. in Levr., Dict. Sci. Nat. 42: 3. 1826.—FIG. 42.

Conyza odorata L., Syst. Nat., ed. 10. 1213. 1759. LECTOTYPE: Antilles, Plumier, Pl. Amer., ed. Burm. *tab. 197*, excl. fig. dext.
C. purpurascens Swartz, Nov. Gen. Sp. Pl. Prodr. 112. 1788. LECTOTYPE: Jamaica, Sloane, Voy. Isl. Madera 2: *tab. 152, fig. 1*. 1725.
Pluchea purpurascens (Swartz) DC., Prodr. 5: 452. 1836.

Erect, aromatic *herb* to 1 m tall; twigs puberulent or cinereous with fine, weak, ascending or spreading hairs, drying faintly many-angled, sometimes reddish. *Leaves* ovate, elliptic or lanceolate, mostly 5–8 cm long, 1.5–3 cm wide, apically acute, mucronulate, basally obtuse, acute or acuminate, often oblique, the margins serrate to subentire, 4–6 veins on each side of the prominent midvein, evenly pubescent above and beneath with short, erect, weak hairs and glandular punctae; petioles mostly 3–5 mm long but sometimes wanting. *Inflorescence* an open panicle of slightly congested, several-headed paniculate clusters, without well differentiated bracts and sometimes with linear, 4–8 mm long bracteoles. *Heads* globose-campanulate, disciform; involucral bracts numerous in several unequal series, indurated, dorsally pubescent, the inner series lanceolate, acute; ray florets purplish, numerous, ca. 5 mm long, the corolla capillary, apically 2–3-dentate, the lobes dorsally papillose, the style slender, papillose, branches basally globose, the ovary cylindrical, pubescent with ascending hairs, copiously glandular; disc florets several, purplish, ca. 5 mm long, the corolla tubular, expanding upwards, glabrous, the lobes dorsally glandular, the anthers ca. 2 mm long, the appendages acute, the basal tails slender, coherent, the style branches slender, pilose, free only at the tips, the style base little expanded, the ovary rudimentary, sterile. *Achenes* reddish brown, the body ca. 1 mm long, with glandular, prominently stramineous ribs, pubescent; pappus of numerous, basally united setose bristles in one series.

Widespread in the Caribbean region and eastern North America, *Pluchea odorata* occurs as an adventive in the Panamanian flora, collected only on Barro Colorado Island in February 1932 and July 1960. It may be recognized by its showy, massive inflorescences of pale purple or mauve flowers and by its aromatic foliage. It grows in fresh- and brackish-water marshes.

The lectotype chosen here consists of an ample line drawing of the species. The plant from which it was drawn may be extant in Paris (P), but Linnaeus saw only the drawing. Similarly, the lectotype chosen for *Conyza purpurascens* consists

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FIGURE 42. *Pluchea odorata* (L.) Cass. Habit (× 3/10). [After *Ebinger* 582 (MO).]

J. M. WILSON

of a black and white illustration. Swartz did not see the plant from which it was drawn and it may be in London (BM).

CANAL ZONE: Barro Colorado Island, *Ebinger* 582 (MO); *Woodworth & Vestal 611* (MO).

43. PTEROCAULON

Pterocaulon Elliott, Sketch Bot. 2: 323. 1823. TYPE: *P. pycnostachyum* (Michx.) Elliott = *P. virgatum* (L.) DC.

Chlaenobolus Cass. in Levr., Dict. Sci. Nat. 49: 337. 1827. LECTOTYPE: *C. virgatum* (L.) Cass. = *Pterocaulon virgatum* (L.) DC.

Herbs; roots stout, black, mostly little branched; stems winged by the leaf bases. *Leaves* alternate, linear to elliptic or obovate, the margins entire or crenate, strongly discolorous, tomentose beneath, glabrate above. *Inflorescences* dense or interrupted terminal spikes of single heads and clusters of heads, the clusters bracteolate. *Heads* disciform, white or yellow; involucral bracts in several series, acute, pubescent, the midvein prominent; ray florets numerous, the corollas capillary, the androecium wanting, the ovary fertile, pubescent, sometimes glandular; disc florets several, the corollas tubular, 5-lobed, the anthers appendaged, the basal auricles connate or distinct with short, fine tails, the style branches lanceolate, pubescent, the style base expanded, situated on a thickened stipe, the ovary rudimentary. *Achenes* dark, plump, with conspicuous ribs which continue into the pappus; pappus of numerous fine bristles in 1 series, slightly united basally.

The circumscription of *Pterocaulon* poses difficulties. Many species have been described from the southern hemisphere of the Old World which appear at least superficially distinct and which appear to belong under *Monarrhenus* Cass. (1817) or *Monenteles* Labill. (1825). The many species of *Pterocaulon* described from South America would seem for the most part congeneric with the taxon treated here.

The black roots of these plants have long been of medicinal repute.

In Panama, the genus is best recognized by the green upper leaf surface, the prominently winged stems, and by the small heads amassed in silky, apical cylinders.

1. **Pterocaulon virgatum** (L.) DC., Prodr. 5: 454. 1836.—FIG. 43.

Gnaphalium virgatum L., Pl. Jamaic. Pug. 405. 1759. LECTOTYPE: Herb. Linn. 993.29 (LINN).
Conyza virgata Lam., Encycl. Meth. 2: 93. 1786. TYPE: Carolina merid., Lamarck (P).
C. alopecuroides Lam., Encycl. Meth. 2: 93. 1786. LECTOTYPE: Martinique, "L.B." (P).
Gnaphalium undulatum Walt., Fl. Carol. 203. 1788. TYPE: Carolina, *Walter* (not seen).
Conyza polystachya Michx., Fl. Bor. Amer. 2: 126. 1803. TYPE: not seen.
Pterocaulon polystachyum (Michx.) Elliott, Sketch Bot. 2: 324. 1823.
P. alopecuroides (Lam.) DC., Prodr. 5: 454. 1836.
P. virgatum var. *alopecuroides* (Lam.) Griseb., Cat. Pl. Cub. 150. 1866.
P. undulatum (Walt.) Mohr, Contr. U.S. Natl. Herb. 6: 790. 1901.
P. virgatum f. *alopecuroides* (Lam.) Arech., Anales Mus. Nac. Montevideo 6: 268. 1908; Fl. Uruguay 3: 268. 1908.

Erect *herb* to 1 m tall; stems prominently winged by linear, discolorous leaf-bases; rootstock thick and woody with a black surface. *Leaves* mostly 6–8 cm

long, smaller and narrower near the inflorescence, lanceolate to elliptic, entire or crenate, apically obtuse, basally narrowed at the juncture with the stem, beneath tomentose with buff, cobwebby or crinkled, simple hairs, above glabrate, the principal veins pubescent. *Inflorescence* to 12 cm long and 5 cm across, a terminal, unbranched spike, congested or open, the peduncle not evident, the heads sessile in glomerules or solitary with linear bracts approaching or subtending the glomerules. *Heads* disciform, to 1 cm long; involucral bracts imbricate in several unequal series, acute, tomentose outside, 2–3 mm long, the midrib prominent; ray florets numerous, ca. 10 mm long, the corolla capillary, apically 4-denticulate, slightly expanded at the base, the style branches slender, slightly exserted, the style base hemispherical, the ovary cylindrical, densely hirsute with ascending hairs; disc florets several, 7–8 mm long, the corolla tubular, 6–7 mm long, apically irregularly 5-lobed, the lobes ca. 1 mm long, the anthers ca. 1 mm long, the appendages blunt, the basal auricles connate with filiform, short, crumpled tails, the style branches lanceolate, dorsally puberulent, the style base expanded, situated on a thickened conical stipe, the ovary rudimentary, pubescent with weak spreading hairs. *Achene* orange-brown, ca. 1 mm long, plump, with prominent, straminous ribs, hirsute with ascending hairs, glandular; pappus white to stramineous, of numerous slender bristles 8–11 mm long in 1 series.

This species is rare in Panama. It is a sporadic weed of the Caribbean area. North American and Antillean plants have usually been separated as *P. alopecuroidies* and *P. undulatum*, but the differences, if any, are not apparent. The name *Pterocaulon virgatum* has often been restricted to plants having a slender elongate spike of interrupted heads. While strikingly different on the herbarium sheet, such plants are not specifically distinct.

PANAMÁ: Hills above Campana, 600–800 m, *Allen 1325* (MO).

44. TESSARIA

Tessaria Ruiz & Pavon, Fl. Peru 112, *tab. 24.* 1794. LECTOTYPE: *T. integrifolia* Ruiz & Pavon.

Trees or *shrubs* of streams or swamps; stems glabrate. *Leaves* alternate, simple, entire or dentate, sessile or petiolate, appearing glabrous but with the surface minutely glandular, often appearing punctate, and covered with a dense, minute tomentum. *Inflorescence* a terminal panicle, open or congested; bracts scalelike, culculate, broad and unlike the leaves; pedicels pubescent. *Heads* disciform; involucral bracts ovate in several unequal, imbricate series, often pubescent and with scarious margins, the innermost narrow and paleaceous, deciduous with the flowers, the outermost persistent, minute; receptacle convex or concave, sometimes obscured by the palea; paleas persistent, scalelike basally, often divided into pappuslike bristles which reach the tips of the corollas; ray florets numerous, the corolla capillary, apically 4–5-notched, often unequally so, the ovaries fertile, somewhat dorsally flattened with a pappus of slender bristles, strigose in the lower portion, sometimes expanded apically; disc florets mostly solitary, the corolla campanulate, the tube short, indistinct from the deeply lobed, tubular limb, the lobes oblong-obtuse, mucronate, making up about half the length of the flower, the

FIGURE 43. *Pterocaulon virgatum* (L.) DC.—A–B. Habit (× ⅖).—C. Achene (× 7½). [After *Allen 1325* (MO).]

anthers mostly exserted, basally auricled with crumpled, fimbriate tissue which may be derived from taillike appendages, apically 5-lobed and mucronate, the distinction between anther and apical appendage not clear, the style apically thickened into a fusiform, glandular, papillose-pubescent area of stylar branches which separate unequally only apically or not at all, slightly contracted at the point of insertion, the ovary nearly obsolete except for the large, cylindrical, apically lobed nectary and the basally scalelike pappus which separates part way up into slender, strigose bristles.

Tessaria is a genus of 3–4 species of Central America and South America ranging to Argentina. In Central America, only the type species, *T. integrifolia* is known, and this species ranges to Peru. Other species are all south of Panama. The species from Texas and Mexico known as *T. sericea* (Nutt.) Shinners is not congeneric with *T. integrifolia* and must be assigned a different name.

Tessaria is singular in the large nectary of the solitary disc floret. Superficially this looks like the ovary with the pappus attached to the bottom. This well-developed pappus is actually inserted on the rudimentary ovary below. Dried species of *Tessaria* usually have smooth, or wrinkled greyish leaves which appear somewhat coriaceous.

Literature:

Robinson, H. & J. Cuatrecasas. 1973. The generic limits of *Pluchea* and *Tessaria* (Inuleae, Asteraceae). Phytologia 27: 277–285.

1. **Tessaria integrifolia** Ruiz & Pavon, Syst. Veg. 213. 1798. TYPE: Peru, ?*Dombey s.n.* (P-Jussieu, not seen).—FIG. 44.

Conyza riparia H.B.K., Nov. Gen. Sp. Pl. 4: 76. 1820. TYPE: not seen.

Tree or *shrub* to 10 m tall; twigs drying chocolate brown, puberulent, soon glabrescent. *Leaves* entire or denticulate, oblanceolate or elliptical, mucronulate, to 9 cm long, 2.5 cm wide, basally narrowed, apically acute, mucronulate, with ca. 5 pinnate veins on each side of the midvein, drying grey or yellowish green, canescent, ?glandular when young, glabrescent in age and then with a waxy, punctate patina of dense hairs; petiole 5–10 mm long. *Inflorescence* an open, cymose panicle, the pedicels slender, thickening in fruit, puberulent-pulverulent, the heads grouped in somewhat compacted clusters; bracts and bracteoles scale-like, broad, resembling the lowermost involucral bracts, appressed pubescent. *Heads* disciform ca. 4 mm long, campanulate; involucral bracts in 3–5 tightly appressed imbricate series, ochraceous, indurate, scarious margined, sparingly pubescent-pulverulent, the innermost lanceolate, glabrous, paleaceous, persistent, the outer series broad, deciduous except for the basal 2 or 3; receptacle conical, ca. 1 mm across, copiously tufted with bristlelike hairs, alveolate, the punctae well separated; ray florets many, the corolla capillary, ca. 3 mm long, basally expanded and lighter colored around the nectary, apically notched, sometimes with a rudimentary lobe or ligule, the style exserted for part of its united portion, the branches long exserted, linear, puberulent, basally with a small but distinct nectary of a lighter color than the style; disc floret solitary, much larger than the

A
B

ray florets, the corolla tube short, the limb fusiform, divided halfway into acute lobes which are dorsally angled, with a large, 1-mm long, achene-like swelling around the nectary, this portion contracted apically, the base of the tube slightly expanded to give the appearance of a false nectary, the anthers basally sagittate, the adjacent tails united, entire, the pointed appendages not differentiated in texture, acute, exserted for half their length, the style with a large (1 mm long) basal, apically lobed nectary, the style branches not separating, exserted, uniformly cylindrical, much thicker than those of the ray flowers, apically capitate or not, short pubescent, the ovary rudimentary, minute, the pappus sturdy, of strigose bristles which recurve outwards and then upwards from the united base, much larger and sturdier than those of the ray flowers. *Achenes* (of ray flowers) light brown, ca. 0.5 mm long with somewhat irregular rounded angles; carpopodium prominent, lighter colored; pappus of nearly smooth white bristles, basally united and flaring.

Tessaria integrifolia may be recognized by its subcoriaceous, subentire leaves which dry with a greyish or yellowish cast. The solitary large disc floret with its large stylar nectary is notable.

CHIRIQUÍ: 2 mi SW of Puerto Armuelles, *Croat 22076A* (MO). DARIÉN: Road from El Real to Pinogana, *Duke 5017* (MO, NY).

V. HELIANTHEAE

Heliantheae Cass., Jour. Phys. 88: 189. 1819. TYPE: *Helianthus* L.

Ambrosieae Cass., Jour. Phys. 88: 191. 1819. TYPE: *Ambrosia* L.
Madieae Jepson, Fl. West. Middle Calif. 486. 1901. TYPE: *Madia* Mol.
Iveae Rydb., N. Amer. Fl. 33(1): 3. 1922. TYPE: *Iva* L.

Mostly *herbs*, sometimes *shrubs*, *trees* or *vines*, pubescence of several types often including a characteristic rugose hair (Fig. 1). *Leaves* alternate or opposite, commonly opposite in lower, vegetative portions and alternate near the inflorescence, simple or compound, the margins entire, toothed or lobed, sometimes dissected; petiolate or sessile. *Inflorescence* scapose, paniculate, or often of solitary, long-stalked terminal heads which may form ill-defined aggregates; bracts or bracteoles sometimes present. *Heads* mostly radiate but sometimes discoid, rarely disciform; involucre of few to many, mostly imbricate bracts, usually in several series but sometimes only of 2 dissimilar series (one a calyculus) the innermost often associated with the outer achenes; receptacle flat to conical, mostly paleaceous, the paleas usually costate and enfolding the ovaries; florets mostly dimorphic, the inner or the outer ovaries often abortive; ray florets with 2–3-denticulate or entire rays, the stamens rarely free, mostly appendaged, basally auriculate or sagittate, the style mostly branched, the branches truncate or

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FIGURE 44. *Tessaria integrifolia* Ruiz & Pavon.—A. Habit (× ½).—B. Central floret; pappus at base of large nectary is subtended by a rudimentary ovary (× 6⁹⁄₁₀). [After *Allen 5096* (MO).]

rounded, sometimes appendaged, the shaft often basally expanded above a short stipe, the ovary often compressed, a cupular nectary often present. *Fruit* a relatively large, simple achene, often compressed, sometimes angled or winged, pappus of scales, awns, or bristles; or achene associated with paleas, involucral bracts, or rarely with other florets, and falling as a baccate or utriculate fruit, often as an aggregate.

This tribe is often best recognized by its combination of opposite leaves and yellow florets (distinct from Eupatorieae and Vernonieae) and its numerous graded involucral bracts (distinct from most Senecioneae). The usually well developed paleas are also characteristic. The pappus is seldom of numerous, strigose bristles. This tribe is best developed in the Americas and several subtribes are restricted to the Western Hemisphere.

Literature:

Stuessy, T. F. 1973. A systematic review of the subtribe Melampodiinae (Compositae, Heliantheae). Contr. Gray Herb. 203: 65–80.

a. Leaves both alternate and finely dissected; heads small and flat, less than 3 mm tall.
  b. Male and female florets in separate heads; anthers free; female florets apetalous, solitary; inflorescence a spike ---------- 54. *Ambrosia*
  bb. Both male and female florets in each head; anthers connate; female florets with corolla, more than 1 in a head; inflorescence a much-branched panicle ---------- 55. *Parthenium*

aa. Leaves opposite, or if alternate than not finely dissected; heads often larger.
  c. Disc florets sterile; achenes mostly plump, rounded, not compressed; pappus mostly wanting or minute; paleas present or not; heads radiate or disciform; leaves mostly simple.
    d. Fruit formed by the entire head with all the bracts; florets 9 or fewer; paleas wanting; involucre apically closed at fruit fall.
      e. Fruit samaroid, the achene(s) enfolded by 2(–4) flat, rotund, winglike bracts ---------- 45. *Delilia*
      ee. Fruit baccate, the achene enfolded by fused, thickened, leathery bracts ---- 46. *Milleria*
    dd. Fruit an individual achene, sometimes enclosed by bracts; florets often more than 9; paleas mostly present; involucre apically open.
      f. Vine; leaves trifoliolate; achene compressed ---------- 81. *Hidalgoa*
      ff. Herbs, shrubs, or trees; leaves simple; achene plump.
        g. Leaves conspicuously lobed; large stout herbs to 2.5 m tall; heads more than 1.5 cm across ---------- 52. *Polymnia*
        gg. Leaves serrate, entire, or shallowly lobed; small herbs, if tall then slender; heads less than 1 cm across.
          h. Fruits with stout, hooked spines ---------- 47. *Acanthospermum*
          hh. Fruits without spines.
            i. Shrubs; heads in panicles; florets white.
              j. Achene glabrous; ray florets 2 ---------- 50. *Ichthyothere*
              jj. Achene pilose; ray florets more than 2 ---------- 49. *Clibadium*
            ii. Herbs; heads solitary or in dense clusters; florets yellow.
              k. Leaves short-petiolate (to 5 mm) or sessile; herbs to 60 cm tall; involucral bracts green all over.
                l. Achene smooth, not fused to involucral bracts; petioles pilose ---- 53. *Unxia*
                ll. Achene enveloped in an involucral bract, fruits tuberculate, involucral bracts blunt ---------- 51. *Melampodium*
              kk. Leaves prominently petiolate; slender branched herbs to 2 m tall; involucral bracts drying yellowish or with green tips ---------- 48. *Baltimora*

  cc. Disc florets fertile (sterile in trifoliolate *Hidalgoa*); achenes often compressed or angled; pappus often well developed; paleas present; heads radiate or discoid; leaves simple or compound.

m. Ray corolla ligulate and lacking a tube, persistent and falling with the achene.
n. Paleas puberulent; outer involucral bracts narrow, spreading, inner bracts shorter, valvate, and subtending the ray florets ..... 56. *Heliopsis*
nn. Paleas apically fimbriate-tomentose; involucral bracts all broad, imbricate, appressed, in 2–4 series ..... 57. *Zinnia*
mm. All corollas (ligulate or tubular) with a tube, deciduous before the achene matures.
o. Heads mostly sessile in the leaf axils.
p. Leaves strongly discolorous, grey tomentose beneath, glabrate above ..... 83. *Trichospira*
pp. Leaves similar on each side.
q. Leaves copiously glandular beneath; involucral bracts wide-spreading from near the base ..... 59. *Eleutheranthera*
qq. Leaves eglandular; involucral bracts applied to the head, spreading slightly at the tips ..... 82. *Synedrella*
oo. Heads on stalks more than 5 mm long.
r. Leaves alternate or if opposite, then glandular beneath.
s. Leaves opposite, mostly glandular beneath.
t. Herbs mostly less than 60 cm tall; leaves narrow ..... 25. (*Isocarpha*)
tt. Herbs or shrubs more than 60 cm tall, erect; leaves broad.
u. Pappus of numerous bristles ..... 84. *Calea*
uu. Pappus of a single, short, deciduous awn ..... 63. *Montanoa*
ss. Leaves alternate, eglandular.
v. Heads large, involucre more than 2 cm across; peduncles long, apically thickened, hollow; leaves deeply lobed ..... 71. *Tithonia*
vv. Heads smaller, involucre less than 1.5 cm across; peduncles solid, not apically enlarged, mostly short; leaves serrate to entire.
w. Outer involucre of narrow, scalelike bracts; achene winged.
x. Shrubs or trees; pappus of two small awns ..... 72. *Verbesina*
xx. Low herbs; pappus wanting ..... 78. *Chrysanthellum*
ww. Outer involucre of 5 broad, foliaceous bracts; achene not winged ..... 67. *Sclerocarpus*
rr. Leaves opposite, eglandular.
y. Pappus of flat, strigose, or plumose bristles.
z. Leaves deeply toothed or divided; herbs less than 60 cm tall ..... 88. *Tridax*
zz. Leaves serrate; herbs or shrubs more than 60 cm tall ..... 84. *Calea*
yy. Pappus of awns, scales, or wanting.
A. Leaves mostly pinnately compound or trifoliolate; fruits often awned.
B. Heads large, involucre more than 20 mm across; ligules numerous in several series, often sterile; pappus poorly developed or wanting ..... 80. *Dahlia*
BB. Heads smaller, involucre mostly less than 20 mm across; ligulate florets in only 1–2 series, fertile; pappus of barbed awns, rarely wanting.
C. Achenes narrowed into a beak distinct from the body; leaves deeply dissected, mostly more than 3 cm long ..... 79. *Cosmos*
CC. Achenes sometimes narrowed but without a distinct beak; leaves mostly trifoliolate, if dissected then mostly less than 3 cm long.
D. Achenes linear with prominent, retrorse-strigose awns; without petiolar hooks; disc florets fertile ..... 77. *Bidens*
DD. Achenes compressed-rectangular, often without awns; climbing by petiolar hooks; disc florets abortive ..... 81. *Hidalgoa*
AA. Leaves simple, mostly serrate to entire; fruits awned or not.
E. Receptacle conical or cylindrical; small or sprawling herbs or vines.
F. Achene compressed, the angles ciliate.
G. Heads solitary on long peduncles, sometimes clustered; heads more than 6 mm across ..... 70. *Spilanthes*
GG. Heads in small, many-headed inflorescences; heads less than 6 mm across ..... 66. *Salmea*
FF. Achene terete or slightly compressed, eciliate.
H. Involucral bracts equal or subequal, in 1(–2) series, lanceolate-linear, basally expanded into wings ..... 86. *Jaegeria*

HH. Involucral bracts unequal, in 2–many series, imbricate, ovate, unwinged.
I. Heads with 3–8 ray florets, each enclosed by an involucral bract and 2–3 paleas; annual herb, mostly erect ---- 85. *Galinsoga*
II. Heads with 8–17 florets, these usually not enclosed by involucral bracts or paleas; annual or perennial herb, mostly prostrate or sprawling ---- 87. *Sabazia*

EE. Receptacle flat or convex; herbs, shrubs, trees, or vines.
J. Outer involucre of 5 linear-spatulate, spreading bracts bearing conspicuous, stalked glands; rugose hairs wanting ---- 68. *Sigesbeckia*
JJ. Involucre not as above; rugose hairs mostly present.
K. Paleas of slender, apically barbed bristles ---- 58. *Eclipta*
KK. Paleas broader, enfolding the achene, not apically barbed.
L. Heads discoid, ray florets wanting.
M. Heads solitary; leaves scabrous ---- 62. *Melanthera*
MM. Heads in small, compact inflorescences; leaves smooth ---- 60. *Garcilassa*

LL. Heads radiate.
N. Pappus wanting.
O. Ray florets fertile; involucre of ca. 5 broad, spreading, foliaceous bracts, the inner bracts different, smaller than the outer bracts ---- 65. *Rumfordia*
OO. Ray florets sterile; involucre not as above, the inner bracts usually longer than the outer bracts.
P. Involucral bracts obtuse; leaves coriaceous; high climbing vine ---- 75. *Wulffia*
PP. Involucral bracts narrowly lanceolate; leaves chartaceous; herbs or erect shrubs ---- 73. *Viguiera*

NN. Pappus present.
Q. Ray florets sterile.
R. Leaves 1-veined or 3-veined from well above the base; inner involucral bracts expanded from the basal, indurate portion; outer bracts 1-costate ---- 64. *Oyedaea*
RR. Leaves 3-veined from near the base; inner involucral bracts not expanded; outer bracts ecostate or several-veined.
S. Achene compressed and conspicuously recessed between the pappus of two awns; involucral bracts copiously ciliate apically; pedicels apically pilose with coarse, spreading hairs and short, often glandular hairs ---- 69. *Simsia*
SS. Achene compressed or terete, apically truncate, pappus of both awns and scales; involucral bracts with mostly glabrate tips; pedicels mostly appressed pubescent or glabrate ---- 73. *Viguiera*

QQ. Ray florets fertile.
T. Outer achene with conspicuous wings.
U. Achene laciniate-winged; heads sessile or nearly so in the leaf axils ---- 82. *Synedrella*
UU. Achene wings sometimes slightly indented but not laciniate; heads long pedunculate, solitary.
V. Leaves pinnately veined ---- 76. *Zexmenia*
VV. Leaves 3-veined from the base ---- 74. *Wedelia*
TT. Achenes without conspicuous wings.
W. Achene with prominent, persistent, strigulose awns ---- 61. *Lasianthaea*
WW. Achene with weak, small awns or scales, or without pappus.
X. Pappus of short, broad scales ---- 87. *Sabazia*
XX. Pappus of 1–2 short, weak, often deciduous awns ---- 74. *Wedelia*

A. MILLERIINAE[20]

TOD F. STUESSY[21]

Milleriinae Benth. & Hook. Gen. Pl. 2: 190. 1873. "Millerieae." TYPE: *Milleria* L.

45. DELILIA[22]

Delilia Spreng., Bull. Sci. Soc. Philom. Paris, sèr. 3, 10: 54, *tab.* 2. 1823. TYPE: *D. berteri* Spreng. = *D. biflora* (L.) Kuntze.

Elvira Cass., Dict. Sci. Nat. 30: 67. 1824. TYPE: *Milleria biflora* L.
Meratia Cass., Dict. Sci. Nat. 30: 65. 1824, nom. superfl., based on type of *Delilia* Spreng.

Annual *herbs*; stems much-branched. *Leaves* opposite. *Inflorescence* of numerous or few, terminal or axillary heads, often in fascicles or glomerules. *Heads* small, radiate; involucre flattened, the bracts 2(–4), slightly herbaceous, with the exterior bract conspicuously larger than the rest; receptacle small, naked; ray florets 1–3, carpellate, fertile, the corollas yellow (to white), the tube and ligule narrow, subentire; disc florets 1–4, perfect, the corollas tubular, 5-lobed, yellow, the throat narrowly campanulate, the anthers 5, entire at the base, the style undivided, hirtellous, the ovary sterile. *Achenes* obovate, flattened, smooth, glabrous, completely enclosed by the involucral bracts; pappus rudimentary. Chromosome number $n = 12$.[23]

Delilia is a genus of 3 species with the most common one, *D. biflora*, widely distributed throughout Latin America. The other 2 taxa are restricted to the Galapagos Islands.

The name *Elvira* has been used most often for this genus. The competing name, *Delilia*, was believed by many workers to have been published by Sprengel in 1826 (Syst. Veg., ed. 16, 3: 367), two years after Cassini's publication (1824) of *Elvira*. However, in addition to the 1826 description, Sprengel also published the name *Delilia* three years earlier (1823) in the Bull. Sci. Soc. Philom. Paris.

1. **Delilia biflora** (L.) Kuntze, Rev. Gen. Pl. 333. 1891.—FIG. 45.

Milleria biflora L., Sp. Pl. 919. 1753. TYPE: Mexico, "Habitat in Campechia," date and collector unknown, Herb. Linn. 1031.4 (LINN, holotype, not seen, IDC 177.621.I.5).
Delilia berteri Spreng., Bull. Sci. Soc. Philom. Paris, sèr. 3, 10: 54, *tab.* 2. 1823. TYPE: Colombia, Magdalena, "ad flumen S. Magdalenae in America australi inventa," *Bertero s.n.* (P?, holotype, not seen).
Elvira martyni Cass., Dict. Sci. Nat. 30: 68. 1824, nom. superfl., based on type of *Milleria biflora* L.

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[20] Support for this investigation under NSF Grant GB-37678 is gratefully acknowledged.
[21] Department of Botany, The Ohio State University, Columbus, Ohio 43210.
[22] Generic description adapted from Bentham & Hooker (1873: vol. 2: 343).
[23] Chromosome numbers for the genera and species listed in this portion of the *Flora of Panama* have been obtained from the standard chromosomal indexes (Darlington & Wylie, 1955; Fedorov, 1969; Cave, 1956–1964; Ornduff, 1965–1967; Moore, 1969–1970).

Meratia sprengelii Cass., Dict. Sci. Nat. 30: 66. 1824, nom. superfl., based on type of *Delilia berteri* Spreng.
Elvira biflora (L.) DC., Prodr. 5: 503. 1836.

Annual *herbs*, 1–9 dm tall; stems erect, 1–4 mm diam., glabrate to antrorsely strigose with hairs 0.5 mm long. *Leaves* narrowly ovate, 3–8 cm long, 1.5–3 cm wide, acute to acuminate, the base attenuate, both surfaces strigillose with hairs 0.3–0.5 mm long, the margin serrate; petioles 3–12 mm long and 0.5 mm diam. *Inflorescence* globose terminal and axillary clusters (approaching a secondarily headed condition); peduncles 1–2 mm long. *Heads* radiate, 4–5 mm tall, 3.5–5 mm wide; involucre compressed, completely enclosing the florets, of three herbaceous strigillose bracts, one large and two small, the large bract ovate, 4–5 mm long, 3.5–5 mm wide, the apex rounded, the smallest bract narrowly ovate, 3 mm long, 1 mm wide, the apex acute, hidden beneath the slightly larger middle-sized bract; paleas absent; ray floret 1, the ligule ovate, 0.4 mm long, 0.3 mm wide, the tube 1.3 mm long, 0.1 mm diam., glabrous; disc floret 1(–4), the corolla 0.6 mm diam., the throat 1 mm and tube 1.5 mm long, glabrous, the anthers black, the ovary filiform, 1.5 mm long, 0.1 mm diam. *Achene* obovoid, gray, compressed, with a central ridge, 2–2.5 mm long, 1.2–1.4 mm diam., glabrous. Chromosome number $n = 12$.

This species is easily distinguished from other taxa of the Heliantheae by the axillary and terminal clusters of samaralike involucres. It flowers from October to March.

CANAL ZONE: Transisthmian Hwy., ca. 19 mi from Colón, *Burch et al. 1007* (DUKE, F, GH, MO, NY, UC, US). Las Sabanas, *Celestine 112* (US). Madden Dam, *Ebinger 861* (MO). Between Summit and Gamboa, *Greenman & Greenman 5249* (GH, MO). Paraíso Station, *Hayes 170* (GH). Las Cruces Trail, 75 m, *Hunter & Allen 688* (MO). Río Grande, near Culebra, 50–100 m, *Pittier 2127* (US). Balboa, *Standley 26411* (GH, US). Gamboa, *Standley 28363* (US). Pueblo Nuevo, *White 302* (GH, MO). Ca. 1 mi SW of Cocoli, *Wilbur et al. 12868* (F, DUKE, GH, NY). COCLÉ: ½ mi from El Copé, *Correa 398* (MO). Near El Valle de Antón, *Croat 13288* (MO). El Valle de Antón, 1000–2000 ft, *Lewis et al. 2590* (DUKE, MO, UC). LOS SANTOS: Ca. 5 mi S of Las Tablas, *Burch et al. 1250* (GH, MO, UC, US). 25 mi SW of Tonosí, 2500–3000 ft, *Lewis et al. 2890* (DUKE, MO, NY, UC). 16 mi S of Macaracas at Quebrada Bejuco, *Tyson et al. 3094* (MO). PANAMÁ: Ca. 1 mi N of Chagres River along Boyd Roosevelt Hwy., *Blum & Tyson 1983* (MO). Between Capira and Potrero, 80–130 m, *Dodge & Hunter 8620* (MO). Cerro Campana, 650 m, *Kennedy et al. 2034* (MO). VERAGUAS: 1–2 mi above Santa Fe, *Gentry 3065* (MO). Montijo, 8 mi S of Santiago, *Tyson 6033* (DUKE).

46. MILLERIA[24]

Milleria L., Sp. Pl. 919. 1753. Gen. Pl., ed. 5. 390. 1754. TYPE: *M. quinqueflora* L.

Tall branching *herbs*; stems erect. *Leaves* opposite, the upper subsessile, the lower with winged petioles. *Inflorescence* of small heads in terminal racemose panicles. *Heads* radiate; involucre obliquely depressed-subglobose, enlarged after anthesis and enclosing the achene, the bracts few, concave; receptacle small, naked; paleas scarious; ray floret 1, carpellate, fertile, the ligule yellow, trifid at the apex; disc florets 3–5, perfect, the corollas tubular, 5-lobed, green,

[24] Generic description adapted from Bentham & Hooker (1873: vol. 2: 344).

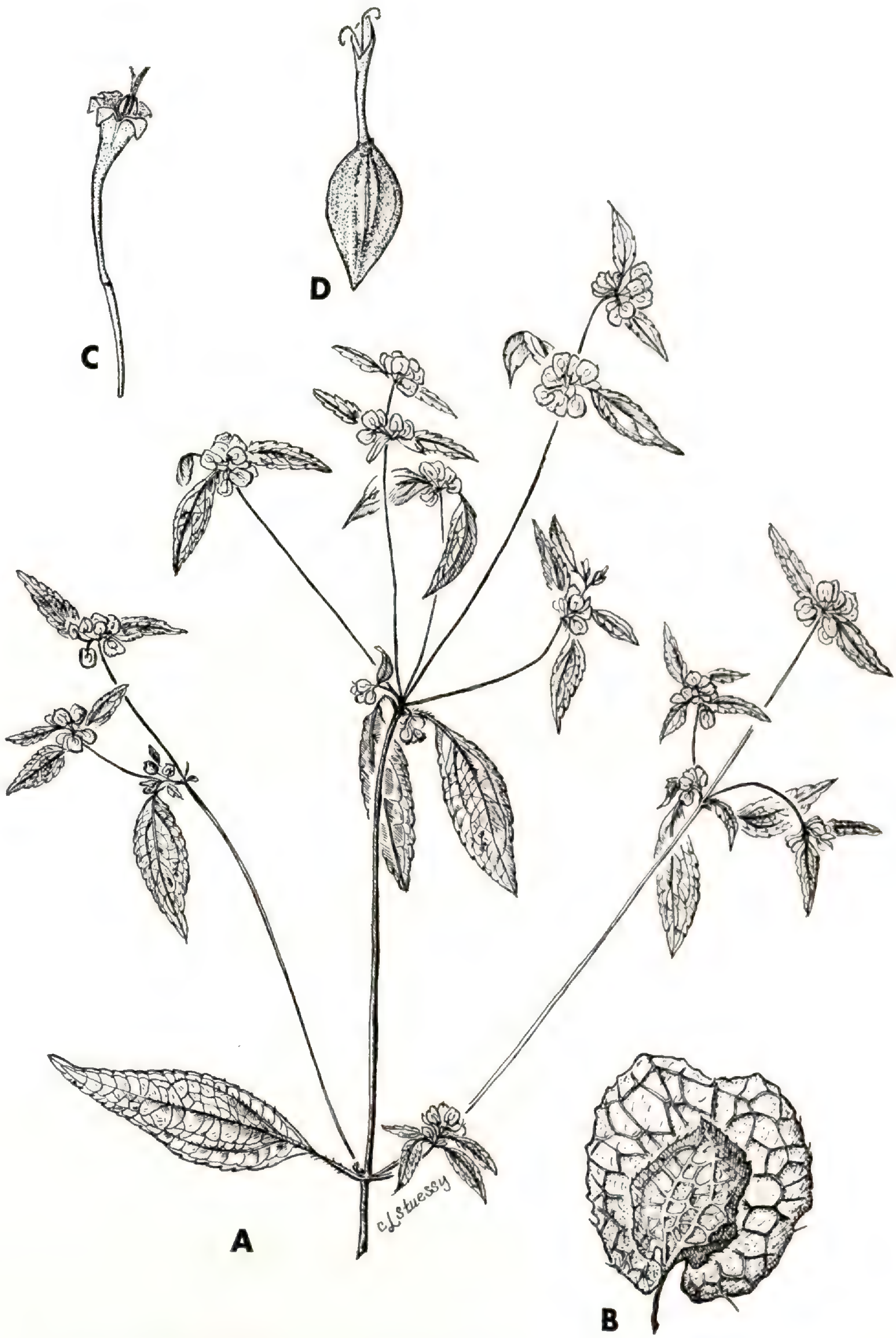

FIGURE 45. *Delilia biflora* (L.) Kuntze.—A. Habit (× ½).—B. Fruiting Head (× 6½).—C. Inner floret (× 8⅛).—D. Outer floret (× 8⅛). [After *Lewis et al.* 2590 (MO).]

FIGURE 46. *Milleria quinqueflora* L.—A. Habit (× 3/5). [After *King 5324* (UC).]—B. Flowering head (× 6). [After *Woodson et al. 1545* (MO).]—C. Fruiting head (× 3½). [After *Crawford 468* (NY).]

the throat campanulate, the anthers 5, the base slightly sagittate, the appendages short, the style undivided, subulate, hirtellous, the ovary sterile. *Achene* ovoid, compressed, smooth, glabrous, enclosed tightly by the involucre at maturity; pappus absent. Chromosome number $n = 15$.

A genus of only one species, distributed from Mexico to Ecuador. *Milleria* in fruit is easily distinguished from other members of the family by the unusual covering of hard involucral bracts around the single fertile achene (Fig. 46C).

1. **Milleria quinqueflora** L., Sp. Pl. 919. 1753. TYPE: Cultivated in Uppsala Botanical Garden, precise locality, date and collector unknown, Herb. Linn. 1031.1 (LINN, holotype, IDC 177.621:1.1).—FIG. 46.

Annual *herbs*, 0.3–1.5 m tall; stems 0.2–0.5 mm diam., glabrous below to copiously stipitate-glandular above with hairs 0.1–0.2 mm long. *Leaves* narrowly ovate to ovate or deltoid, 4.5–18 cm long, 2.8–13 cm wide, acuminate, the base attenuate, often auriculate at base of petiole, marginally serrate, both surfaces glabrate to strigose with hairs 0.1–0.3 mm long; subsessile or with tapering winged petioles 0.3–6 cm long, to 1 cm wide near blade. *Inflorescence* with peduncles 3–9 mm long, stipitate-glandular. *Heads* 3–5 mm tall, 2–3 mm across; involucre of 3 bracts, 2 bracts large, connate and conduplicate around the ray floret, together to 3 mm long and 5 mm wide, with 2 acute lobes, strigillose and stipitate-glandular, the third bract small ovate, 2 mm long, 2 mm wide, the apex acute; paleas 3–5, lanceolate to elliptic, the apex obtuse to rounded, 2 mm long, 0.6–1 mm wide; ray floret 1, the ligule broadly obovate, with 3 deep lobes, 3–5 mm long, 2.5–4 mm wide, resin-dotted on abaxial surface, the tube 0.4 mm long, 0.3 mm diam., glabrous; disc florets 3–5, the corollas green, 1.3 mm diam., the throat 2 mm and tube 1 mm long, glabrous, the anthers black, the ovary filiform, 1.2 mm long, 0.1 mm diam. *Achene* black, 5 mm long, 3 mm diam., glabrous, enclosed tightly and completely by the 3 bracts which become very leathery at maturity. Chromosome number $n = 15$.

This species flowers during most of the year.

CANAL ZONE: Juan Mina, *Bartlett & Lasser 16513* (MO). C-15 road, *Blum & Dwyer 2682* (MO). Colón to Empire, Panama RR, *Crawford 468* (F, GH, NY). Chilibre, *Dwyer 1025* (MO). Gamboa, *Piper 5656* (GH, US). Near Gamboa, 40–80 m, *Pittier 3694* (GH, US). Between Corozal and Ancón, 10–30 m, *Pittier 6737* (US). Gamboa, *Standley 28516* (US). Fort Kobe road, *Woodson et al. 1420* (GH, MO, NY, US). CHIRIQUÍ: Near Puerto Armuelles, 0–75 m, *Woodson & Schery 843* (GH, MO). COCLÉ: Banks of Río Grande, *Burch et al. 1171* (F, GH, MO, NY, UC, US). Behind Club Campestre, ca. 700 m, *Duke 13262* (MO). Ca. 10 mi SE of Antón, *King 5268* (UC, US). W slopes of El Valle, *King 5324* (UC, US). El Valle de Antón and vic., 500–700 m, *Seibert 449* (GH, MO, NY, US). COLÓN: Achiote, *Tyson et al. 4524* (GH, MO). HERRERA: Between El Potrero and Las Minas, *D'Arcy & Croat 4135* (MO). PANAMÁ: Panama City on way to Tocumen, *D'Arcy & D'Arcy 6112* (MO). Ca. 6 mi E of Chepo, *Duke 4083* (GH, MO). About halfway between El Llano and Río Mamoni, *Duke 5601* (MO). Near Río Mar, 5–20 m, *Duke 12424* (MO). Escuela Agronomia, Tocumen, *Dwyer 4035* (MO, US). Just E of Chicá, *King 5261* (UC, US). Las Sabanas, *Standley 25896* (US). Near Juan Franco Race Track, near Panamá, *Standley 27715* (US). Tumbo Muerto road, near Panamá, *Standley 29718* (US). Juan Díaz, *Standley 30494* (US). Isla Taboga, 0–186 m, *Woodson et al. 1545* (GH, MO, NY). VERAGUAS: 2–4 mi E of Santiago, ca. 30 m, *Duke 12350* (MO). 5 mi E of Santiago, *Tyson et al. 4269* (MO).

B. MELAMPODIINAE[25]

Tod F. Stuessy[26]

Melampodiinae Less., Linnaea 5: 149. 1830. "Melampodieae." TYPE: *Melampodium* L.

47. ACANTHOSPERMUM[27]

Acanthospermum Schrank, Pl. Rar. Hort. Monac. *tab.* 53. 1819. TYPE: *A. brasilum* Schrank = *A. australe* (Loefl.) Kuntze.

Annual *herbs*; stems dichotomously branched, pubescent. *Leaves* opposite, subentire to pinnatifid. *Inflorescence* of solitary heads in the axils and forks of the stem. *Heads* radiate; involucre biseriate, the outer bracts 4–6, elliptic to ovate, herbaceous, the inner bracts of the same number as the ray achenes and closely enveloping them; receptacle small, convex, paleaceous; ray florets carpellate, fertile, uniseriate, 5–8, the corollas elliptic to ovate, pale yellow, the apex emarginate or tridenticulate, the tube as long as or much shorter than the limb; disc florets perfect, 3–30, the corollas yellow with a short cylindrical tube, the throat cylindric-funnelform or campanulate, 5-lobed, the anthers barely cordate to cordate-sagittate, the appendage ovate, obtuse, and somewhat inflexed, the style clavate, obtuse, undivided, hispidulous, the ovary sterile, pappus absent. *Fruit* cuneate or oblong-fusiform, rarely trigonous-turbinate, weakly or strongly laterally compressed, more or less densely echinate on the whole surface, the angles with straight or usually uncinate prickles. Chromosome numbers $n = 10, 11$.

This is a genus of 6 species distributed primarily throughout Latin America. One species, *A. hispidum*, has been introduced to many ports of entry throughout the world.

Acanthospermum is a close relative of *Melampodium*, a genus also found in Panama. Both taxa have perfect but sterile disc florets and involucral bracts of the inner series that enclose single ray achenes. The most important feature distinguishing the two genera comes from the fruits which are spiny in *Acanthospermum* and smooth, ribbed, or sculptured in *Melampodium* (cf. Figs. 47B, 52B).

Literature:

Blake, S. F. 1921. Revision of the genus *Acanthospermum*. Contr. U.S. Natl. Herb. 29: 383–392.

Stuessy, T. F. 1970. The genus *Acanthospermum* (Compositae-Heliantheae-Melampodinae): taxonomic changes and generic affinities. Rhodora 72: 106–109.

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[25] Support for this investigation under NSF Grant GB-37678 is gratefully acknowledged.

[26] Department of Botany, The Ohio State University, Columbus, Ohio 43210.

[27] Generic description adapted from Blake (1921).

1. **Acanthospermum humile** (Swartz) DC., Prodr. 5: 522. 1836.—FIG. 47.

Melampodium humile Swartz, Prodr. Veg. Ind. Occ. 114. 1788. TYPE: Jamaica, "Domingo," 1783–1787, *Swartz s.n.* (S, holotype, not seen; B, isotype, TEX, photo).

Annual *herbs*, 15–35 cm tall; stems erect, 1.5–3.5 mm diam., hirtellous to pilose with hairs to 0.7 mm long. *Leaves* lyrate, the margin sinuate especially on the blade, 2–4.5 cm long, 1.2–2.7 cm wide, the apex obtuse, the base attenuate, the upper surface sparingly pilose, the lower surface resin-dotted and sometimes more densely pilose; petiole tapering, winged, 1–2.2 cm long. *Inflorescence* with heads subsessile or with peduncles up to 1 mm long. *Heads* radiate, 3–5 mm tall, 6–10 mm across; outer involucre spreading, 6–7 mm diam., the bracts usually 5, separate, lanceolate to narrowly ovate, 3–4 mm long, 1.5–2 mm wide, apically acute, the abaxial surface resin-dotted and sparingly pilose with hairs 0.5 mm long, the margin herbaceous and ciliate; paleas elliptic, 1 mm long, 0.2 mm wide, apically erose; ray florets 5–7, the ligules light yellow, elliptic, 1 mm long, 0.4 mm wide, apically emarginate; disc florets 3–5, the corollas yellow-orange, 0.7 mm diam., the throat and tube each 0.7 mm long, the ovaries sterile, 0.8 mm long, 0.1 mm diam. *Fruits* 2.5–4 mm long, the sides resin-dotted, the apex with hooked short spines and 2 straight divergent spines to 4 mm long. Chromosome number unknown.

The center of distribution for this species is in the West Indies (especially common in Cuba and Jamaica). It flowers during most of the year.

CANAL ZONE: Chagres, *Fendler 171* (F, GH, US). COLÓN: Between Fato and Playa de Dumas, *Pittier* 3833 (NY, US). CHIRIQUÍ: Boca Chica de Horconcitos, *Pittier 5123* (GH, US).

48. BALTIMORA

Baltimora L., Mant. Pl. 158. 1771. TYPE: *B. recta* L.

Scolospermum Less., Linnaea 5: 152, *tab. 2, figs. 19–31.* 1830. TYPE: *S. baltimoroides* Less.

Erect, annual, taprooted *herbs*; stems terete, obtuse-angled when dry, yellow-green to purple. *Leaves* opposite, acuminate, 3-nerved from near the base, the margin serrate to biserrate, petiolate. *Inflorescence* of axillary and terminal heads in few-flowered racemes or large panicles. *Heads* radiate, subcylindrical to subglobose; involucral bracts of unequal length, in 3 series, narrowly ovate, acute-acuminate, the adaxial surface glabrous, the outer bracts strigose, the margins scarious toward base, the inner bracts becoming less strigose and more scarious; receptacle convex; paleas conduplicate, lanceolate, scarious, glabrous, acute, the apical margin ciliate with hairs 0.3 mm long, the midrib weak; ray florets fertile, the ligules yellow, elliptic, apically emarginate, the undersurface strigose on veins with hairs 0.1–0.2 mm long, the tube glabrous, 0.2 mm diam., the stigmatic lobes 2, 1 mm long; disc florets perfect, the corollas yellow, glabrous, exserted above the paleas at anthesis, the throat funnelform, the lobes partially reflexed, narrowly triangular, 0.2 mm wide, pubescent on the upper surface, the anthers black, auriculate at base, the style filiform, 0.1 mm diam., the stigma yellow, undivided, 0.2 mm diam., the ovary filiform, sterile, 0.2 mm diam., glabrous. *Fruits* triquetrous, sometimes markedly winged, on sides smooth to tuberculate; pappus a crown of tissue or a collar of short awns. Chromosome number $n = 15$.

FIGURE 47. *Acanthospermum humile* (Swartz) DC.—A. Habit (× 3/5).—B. Fruit consisting of achene and a fused involucral bract (× 6 3/10). [After *Pittier 5123* (US).]—C. Head (× 6 3/10). [After *Pittier 5123* (GH).]

Baltimora is a genus of two species distributed throughout Mexico, the West Indies, and South America. Although traditionally placed in the subtribe Melampodiinae, the strongest affinities of the genus may be with *Wedelia* and its relatives in the subtribe Helianthinae.

Literature:

Stuessy, T. F. 1973. Revision of the genus *Baltimora* (Compositae, Heliantheae). Fieldiana, Bot. 36: 31–50.

1. **Baltimora recta** L., Mant. Pl. 288. 1771. TYPE: United States, Maryland, near Baltimore, date and collector unknown, cultivated in Botanical Garden Uppsala (not located).—FIG. 48.

Scolospermum baltimoroides Less., Linnaea 5: 152, *tab. 2, figs. 19–31*. 1830. TYPE: México, "Santa Fe," Jul 1828, *Schiede & Deppe* 335 (B, holotype, not seen, F, MICH, TEX, US, photos).

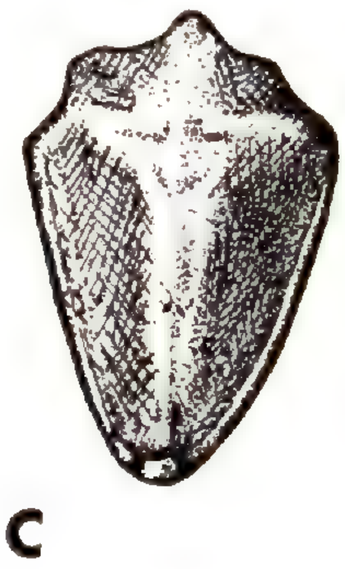
Baltimora scolospermum Steetz in Seem., Bot. Voy. Herald 154. 1854, nom. superfl., based on type of *Scolospermum baltimoroides* Less.

B. scolospermum var. *panamensis* Steetz in Seem., Bot. Voy. Herald 154. 1854. TYPE: Panamá, "in savanas," 1846–1869, *Seemann s.n.* (BM, holotype, not seen; GH, isotype).

Herb, to 3 m tall; stems glabrate at base, moderately to markedly strigose toward apex with hairs 0.3 mm long. *Leaves* broadly to narrowly ovate, 2.5–15 cm long, 1.5–12 cm broad, basally truncate to shortly attenuate, both surfaces weakly to moderately strigose with hairs 0.1–0.3 mm long; petioles 0.8–7 cm long, 0.2–1 mm diam. *Inflorescence* with heads in racemes or more often in large panicles; peduncles 8–33 mm long, 0.3–0.7 mm diam., strigose with hairs 0.3 mm long. *Heads* radiate, 7–22 mm across, 5–8 mm tall; involucral bracts 3–6, 3.5–6 mm long, 1.7–2.2 mm wide, the apical margin ciliate with hairs 0.3 mm long, the outer bracts weakly strigose abaxially with hairs 0.3 mm long; receptacle 1 mm diam.; paleas 3.5–4.2 mm long, 0.6–0.8 mm wide; ray florets 3–8, the ligules 3.8–5.5 mm long, 1.2–3.1 mm wide, the tube 1.2 mm long; disc florets 16 or more, the corolla throat 1 mm long, 0.7 mm diam. with lobes 0.5 mm long, the tube 1 mm long, 0.2 mm diam., the anthers 1.7 mm long with truncate appendages, the style 1 mm long, the stigma 1.2–2.2 mm long, the ovary 2.2–4 mm long. *Achenes* 2.4–3.2 mm long, 1.6–1.9 mm diam., truncate and puberulent; pappus a small crown or cup of tissue. Chromosome number $n = 15$.

Baltimora recta is a weedy species which is found in abundance from Mexico to its southernmost limit in Panama. The achenes of *Baltimora* show striking variations in the ornamentation of the outer pericarp, ranging from nearly smooth (Fig. 48C) to conspicuously winged (Fig. 48D). It flowers throughout the year.

CANAL ZONE: Ca. 1 mi from Miraflores, *Blum 1856* (FSU, MO). Frijoles, *Croat 10381* (MO). Just N of Gamboa gate, *D'Arcy & D'Arcy 6000* (MO). Navy Reservation, N of Gamboa, *Dressler 3216* (DUKE, MO). Sosa Hill, *Duke 4666* (MO). Contractor's Hill, *Dwyer & Lallathin 8805* (MO). Gamboa, Naval Reservation, *Ebinger 486* (MO). Corozal, *Greenman & Greenman 5187* (MO). Barro Colorado Island, *Kenoyer 593* (US). Ancón Hill, 100–200 m, *Killip 12001* (US). Pedro Miguel, *King 5234* (UC, US). Ft. Kobbe, *King 5239* (UC, US). Near Madden Dam, 50 ft, *Lewis et al. 9* (GH, MO, NY, UC). Pedro Miguel, *Piper 5491* (US). Near Gatuncillo, *Piper 5632* (US). Near Culebra, 50–150 m, *Pittier 2232* (US). Between Corozal and Ancón, 10–30 m, *Pittier 6739* (US). Madden Dam, *Porterfield s.n.* (NY). Vista



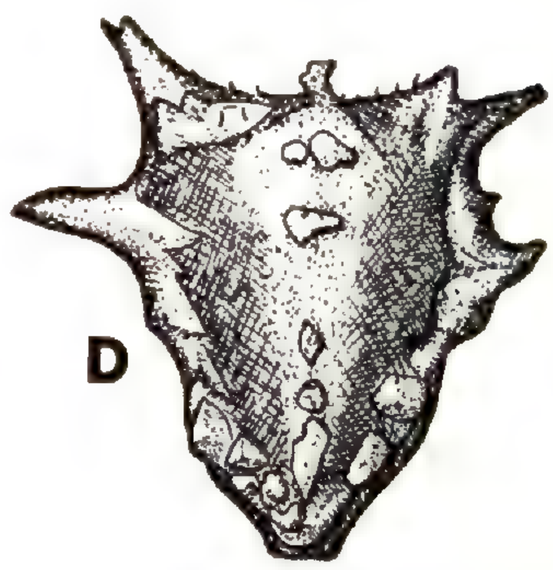


FIGURE 48. *Baltimora recta* L.—A. Habit (× ½).—B. Head (× 2⅘).—C. Achene (× 8³⁄₁₀). [After *Tyson* 6283 (US).]—D. Achene (× 8⁷⁄₁₀). [After *Duke* 5920 (MO).]

del Mar, *Porterfield s.n.* (NY). Sosa Hill, Balboa, *Standley 25278* (US), *26451* (GH, US). Chiva Chiva Trail, Miraflores Lake, *Tyson 1354* (MO). Near Pacific Saddle Club, Pedro Miguel, *Tyson 6283* (FSU, UC). Near Miraflores Lake, *White 246* (GH, MO, US). CHIRIQUÍ: Distrito Guanabano, along Quebrada Guanabano, 0–100 m, *Croat 22540* (MO). Ca. 8 mi W of Las Lajas, grassy roadside, *D'Arcy 5283* (MO). Outskirts of David, *D'Arcy 5289* (MO). Ca. 3 mi above David on way to Boquete, *D'Arcy & D'Arcy 6288* (MO). 10 mi W of Puerto Armuelles, *Liesner 86* (MO). 4 mi S of Puerto Armuelles, 0–100 m, *Liesner 396* (MO). NE of Gualaca, *McCorkle C-42* (FSU, UC). 5 km E of Boca del Monte, *McCorkle C-74* (NY). COCLÉ: Ca. 1 mi E of Antón, *Blum & Tyson 584* (FSU, MO). Nueva Gorgona, *D'Arcy & D'Arcy 6280* (MO). 10 mi E of Natá at Río Grande, *Tyson 5226* (DUKE, FSU). COLÓN: Portobelo, *D'Arcy 4059* (MO). Ca. 1–2 mi N of Colón-Panamá boundary, *Lazor & Tyson 3018* (FSU, UC). Between Río Piedras and Puerto Pilón, *Lewis et al. 3208* (DUKE, MO, UC). DARIÉN: 0–4 mi up river Sabana from Santa Fe, *Duke 4144* (MO). HERRERA: Pesé, ca. 50 m, *Allen 799* (GH, MO, NY). Pan-Am. Hwy. just E of Río Conaca, *D'Arcy & D'Arcy 6669* (MO). Ocú, *Ebinger 1045* (MO). 2 km N of Montijo, *McCorkle C-7* (FSU). PANAMÁ: Near beach at Nueva Gorgona, *Duke 4500* (GH). Near Río Pacora and Chepo Hwy., *Duke 5920* (GH, MO). Pacora, *Dwyer 1232* (MO, UC). Tocumen, *Dwyer 4405* (FSU). Ca. 8 mi S of Goofy Lake, *Dwyer 7053* (GH, MO). Laguna de Portala, near Chepo, 50 m, *Pittier 4588* (US). Between Río Pacora and Chepo, *Porter et al. 5148* (MO). Tocumen Hwy., ca. 3 mi after the airport, *Rivas 14* (DUKE, MO). Nuevo Emperador Hwy., *Rodríguez 22* (DUKE, MO). Corozal Road, near Panamá, *Standley 26826* (US). Macapale Island in Madden Lake, *Tyson 5486* (FSU, MO). VERAGUAS: Hills W of Soná, ca. 500 m, *Allen 1066* (GH, MO). Ca. 5 mi NE of La Mesa, *Blum & Tyson 638* (FSU, MO). 2–4 mi E of Santiago, ca. 30 m, *Duke 12369* (MO). Santiago, 2 mi from Transisthmian Hwy. toward Atalaya, *Dwyer & Kirkbride 7405* (GH, MO, US). 12 mi from Santiago toward Divisa, *Dwyer & Kirkbride 7448* (MO, UC). Puerto Mutis, 12 mi S of Santiago, *Tyson 5193* (DUKE, FSU, MO).

49. CLIBADIUM

Clibadium L., Mant. Pl. 161. 1771. TYPE: *C. surinamense* L.

Shrubs; stems terete to obscurely angular. *Leaves* opposite, lanceolate to cordate, margin serrate or serrulate, petiolate. *Inflorescence* a racemose, corymbose, or capitate panicle, subopppositely branched with subtending bracts decreasing in size to 1.5–2 mm long near heads; heads 8–600, sessile or on short peduncles 0.5–2 mm long. *Heads* inconspicuously radiate; involucre cupulate or funnelform, the bracts 6–13, multiseriate, with outer bracts herbaceous and inner bracts somewhat scarious, usually subequal, imbricate, narrowly ovate to obovate; receptacle slightly convex, 0.5–1.5 mm diam.; paleas mostly absent or less often present; ray florets 3–26, usually uniseriate or less often multiseriate, fertile, the corollas tubular, white, the 2–4 lobes 0.1–0.5 mm long, the styles bifid, pappus absent, sometimes of tufts of hairs (*C. pilonicum*) or of two short awns (*C. asperum*); disc florets 5–22, the corollas tubular, white, with 5 triangular lobes; the anthers black, the style undivided (sometimes slightly parted at tip), with a 5-lobed nectary at base, the ovary sterile, pappus absent. *Achenes* obovoid, brown-black, somewhat compressed radially. Chromosome number $n = 16, 24$.

Clibadium is a genus of approximately 30 species, ranging from Guatemala to southern South America. In Panama the genus has been reported in every province except Los Santos, and the greatest concentration of species (5) occurs in Chiriquí.

Local inhabitants in Panama and Colombia use the vegetative parts of at least some of the species as fish poisons ("barbascos"). The leaves and stems are

beaten into the water releasing polyacetylene compounds that stun the fish and allow for easy capture.

At the present time, despite the existence of two papers that treat *Clibadium* in some detail (Schulz, 1912; Blake, 1917), the basic taxonomy of the genus is confused, and the treatment here must be regarded as provisional.

Clibadium is here included within the subtribe Melampodiinae rather than within the Milleriinae as traditionally placed. Blake (1917) first pointed out the close relationship of *Clibadium* to *Ichthyothere*, a genus conventionally referred to the Melampodiinae, and made the transfer to that subtribe. This decision has recently been substantiated by Stuessy (1973).

Literature:

Blake, S. F. 1917. Notes on the systematic position of *Clibadium*, with descriptions of some new species. Contr. Gray Herb. 52: 1–8.

———. 1924. New American Asteraceae. Contr. U.S. Natl. Herb. 22: 587–661.

———. 1937. Eleven new Asteraceae from North and South America. Jour. Wash. Acad. Sci. 27: 374–391.

Schulz, O. E. 1912. Beiträge zur Kenntnis der Gattung *Clibadium*. Bot. Jahrb. Syst. 46: 613–628.

Stuessy, T. F. 1973. A systematic review of the subtribe Melampodiinae (Compositae, Heliantheae). Contr. Gray Herb. 203: 65–80.

a. Heads with receptacles paleaceous throughout; ray florets multiseriate (B. sect. *Trixidium*) ——— 8. *C. pittieri*

aa. Heads with receptacles naked or only partly paleaceous; ray florets uniseriate (A. sect. *Clibadium*).

b. Leaves with a winged petiole tapering to a subauriculate base ——— 6. *C. subauriculatum*

bb. Leaves with a wingless petiole, at base attenuate to obtuse.

c. Leaves with 3 conspicuous main veins arising from the very base ——— 5. *C. pilonicum*

cc. Leaves with 3 main veins arising 5–30 mm above the base.

d. Mature inflorescence a capitate panicle with groups of 3–6 tightly aggregated heads arranged in a flat-topped cluster ——— 1. *C. anceps*

dd. Mature inflorescence a corymbose or racemose panicle (young inflorescences may appear capitate, but never flat-topped).

e. Leaves over 18 cm wide; heads usually more than 500 in each inflorescence ——— 3. *C. grandifolium*

ee. Leaves 10 cm wide or less; heads usually less than 200 in each inflorescence.

f. Involucral bracts glabrate (sometimes strigillose near apex), often brown-black when dry, ciliate; peduncles and axes of inflorescence densely villous or strigose ——— 4. *C. leiocarpum*

ff. Involucral bracts strigillose to strigose, yellow-green when dry; peduncles and axes of inflorescence moderately strigose or densely hispid.

g. Undersurface of leaves conspicuously reticulately veined and hispid ——— 7. *C. surinamense*

gg. Undersurface of leaves glabrate to strigose ——— 2. *C. asperum*

A. Section CLIBADIUM

Section **Clibadium** (sect. *Euclibadium* DC.)

Paleas absent; ray florets uniseriate.

1. **Clibadium anceps** Greenman, Proc. Amer. Acad. Arts 39: 97. 1903. TYPE: Costa Rica, "Forêts de La Palina," 1459 m, 8 Sep. 1898, *Tonduz 12537* (CR, GH, syntypes, not seen).

Scandent *shrub* 3–6 m tall; stems at least 4 mm diam. (base not seen), antrorsely strigose with hairs 0.3–0.5 mm long. *Leaves* ovate to narrowly ovate, conspicuously 5-veined from near base; blades 10–15 cm long, 4.5–9 cm wide, acuminate, the base obtuse (sometimes shortly attenuate), the margin serrulate, both surfaces glabrate to sparsely strigillose with hairs 0.3 mm long, on midrib and major lateral veins markedly strigose with hairs up to 0.6 mm long; petioles 2–3.3 cm long, 0.7–1.5 mm diam., strigose (markedly so on adaxial side) with hairs up to 0.5 mm long. *Inflorescence* of 56–119 heads in a capitate panicle, with clusters of 3–6 sessile heads terminating all axes. *Heads* radiate; involucre funnelform, 3–4 mm tall, 3–5 mm across, the bracts 5–7, ovate, 3.5–4 mm long, 2–3 mm wide, abaxially strigose with hairs 0.3 mm long, the upper one-third of margin ciliate; paleas absent; ray florets 3–4, the corollas 2.2 mm long, 0.9 mm diam., the 4 lobes 0.2 mm long, the styles 3.3 mm long with the branches 1.8 mm long; disc florets 6–7, the corollas 3.3 mm long, the throat 2.3 mm long and 1 mm diam., the lobes 0.4 mm long, apically comose, the tube 0.4 mm diam., the anthers 2 mm long, the style 5 mm long, the ovary sterile, 2 mm long, 0.3 mm diam., villous (especially at apex) with hairs 0.6 mm long. *Achenes* 2 mm long, 1.2 mm diam., glabrous. Chromosome number unknown.

Clibadium anceps differs from other species of the genus in being scandent as well as in having the lateral branches of the inflorescence more-or-less at right angles to the main axis. The species is somewhat rare in Panama, being found only in Chiriquí. In Panama it flowers in July and August.

CHIRIQUÍ: Cerro Horqueta, 7000 ft, *Blum & Dwyer 2662* (FSU, MO). E side of Cerro Pando (near Río Chiriquí Viejo), 6000 ft, *D'Arcy & D'Arcy 6611* (MO). Palo Alto, E of Boquete, 5000 ft, *Stern et al. 1019* (GH, MO, US).

2. **Clibadium asperum** (Aubl.) DC., Prodr. 5: 506. 1836.

Baillieria aspera Aubl., Hist. Pl. Guiane 2: 804, *tab. 317*. 1775. TYPE: French Guiana, "habitat Caïennae & Guïanae locis incultis," *Aublet s.n.* (BM, holotype, not seen).

Clibadium latifolium Rusby, Descr. S. Amer. Pl. 150. 1920. TYPE: Colombia, Magdalena, "in open places in alluvial forest on banks of river Buritaca, 2 miles from the sea," 28 Sep. 1898, *Smith 2014* (NY, holotype, not seen, US, photo; F, isotype, US, photo).

C. appressipilum Blake, Contr. U.S. Natl. Herb. 22: 600. 1924. TYPE: Panamá: Darién, Boca de Cupe, 13 Apr 1908, *Williams 698* (US, holotype, not seen; NY, isotype, not seen; *Pittier 4730*, GH, US, *Pittier 4157*, US, paratypes).

Shrub 1.5–3 m tall; stems copiously strigillose with hairs 0.1 mm long. *Leaves* ovate; blades 6–22(–28) cm long, 3–10 cm wide, acuminate, the base attenuate, the margin serrate, both surfaces moderately strigillose with hairs 0.1 mm long (longer and more abundant on major veins); petioles 1.5–7 cm long, to 1.5 mm diam., strigillose with hairs 0.1 mm long. *Inflorescence* a corymbose panicle of 25–100 heads; peduncles 1–2 mm long. *Heads* radiate; involucre cupulate, 4–6 mm across, the bracts 7–10, ovate to obovate, 3–4 mm long, 2–3 mm wide, abaxially strigose with hairs 0.2 mm long; paleas absent; ray florets 5–9, the corollas 1.5–2.2 mm long, 0.4 mm diam., the 3 lobes 0.4 mm long, the styles 2.2–2.6 mm long with

branches 1 mm long; disc florets 9–22, the corollas 2.5 mm long, the throat 2 mm long and 0.8 mm diam., the lobes 0.6 mm long, pubescent abaxially with hairs less than 0.1 mm long, the tube 0.3 mm diam., the anthers 1.3 mm long, the style 4 mm long, the ovary sterile, 1.3 mm long, 0.3 mm diam., villous (sometimes only toward apex) with hairs to 0.5 mm long. *Achenes* 1.7–2 mm long, 1.5 mm diam., more convex on abaxial surface, puberulent at apex with hairs to 0.1 mm long; pappus absent or of 2 short awns to 0.6 mm long. Chromosome number unknown.

One collection, *Lewis et al.* 3382, has leaves with longer teeth, heads that are smaller and less tightly aggregated than usual, and longer pappus awns. Despite these differences, the collection appears to belong in *C. asperum*.

The determination of the earliest applicable name for this taxon is mired in difficulty. I have selected a very early name, *C. asperum*, which, judging from the protologue (including the plate, which is taken to represent the holotype), appears to apply to this taxon as found commonly in Panama and in northern South America. Blake (1917) has pointed out a possible confusion in application of the name *C. asperum* with *C. sylvestre*, also described by Aublet in the same publication (both as species of *Baillieria*). Not having seen the types in question, I cannot comment on all of Blake's remarks, but I do not agree with his contention that *C. asperum* is synonymous with *C. surinamense*. The plant figured in plate 317 of Aublet appears to be not *C. surinamense*, but instead is the species treated here. The large ovate leaves with attenuate bases and nonreticulate under-surfaces are not to my knowledge ever found in *C. surinamense*.

This species flowers primarily from May to September and occasionally during the rest of the year.

CANAL ZONE: Barro Colorado Island, *Bailey & Bailey 390* (F); *Croat 12283* (DUKE, F, MO, NY). Vic. of Madden Dam near Río Chagres, 50–75 m, *Seibert 559* (GH, MO, NY, US). CHIRIQUÍ: 10–11 mi W of Puerto Armuelles near San Bartolo Limite, 300–500 m, *Croat 22017* (MO). Quebrada Quanabanito beyond La Repressa, 2 mi SW of Puerto Armuelles, 0–200 m, *Croat 22069* (MO). Distrito Baru along ridge above Brazo Seco, near Costa Rica border, 100–200 m, *Croat 22557* (MO). COLÓN: Near Río Piedras along road to Portobelo, *Blum et al. 2508* (FSU, MO). 1 mi E of Puerto Pilón, *Correa & Haines 234* (MO). ¼ mi N of Maria Chiquita on road to Portobelo, *Croat 11364* (MO). 2 mi S of Portobelo along river, *Croat 11419* (MO). W side of Portobelo, *D'Arcy 4077* (MO). Santa Rita Ridge, *D'Arcy & D'Arcy 6168* (MO). Ca. 1 mi W of Portobelo, *Gentry 1737* (MO, NY). Peluca, ca. 27 km from Transisthmian Hwy. on road to Nombre de Díos, *Kennedy 2629* (MO). Ca. 6 mi SE of Portobelo, *Luteyn 1425* (DUKE). Achiote, *Tyson et al. 4531* (FSU, GH, MO). 5 mi NE of Sabanita towards Portobelo, *Wilbur & Luteyn 11615* (DUKE). 6 mi SW of Portobelo, *Wilbur & Luteyn 11660* (DUKE). DARIÉN: Near Yape, ca. 30 m, *Allen 857* (F, GH, MO, NY, US). Río Chico, near Yaviza, 100 ft, *Allen 4582* (GH, MO). Near Boca Quebrada Venado, Río Tuqueza, *Bristan 1110* (MO). Near El Real, along road to Pinogana, *Croat & Porter 15474* (MO). Río Pirre, *Croat & Porter 15520* (MO). Río Pirre below Río Peresenico, *D'Arcy 5523* (MO). 2–3 mi SE of El Real, *Duke 4838* (GH, MO). Peak ca. 300 ft high between Río Balsa and Río Aretí at their confluence, *Duke 8733* (GH, OS, US). Río Mortí, ca. 6 mi upstream from Mortí Abajo, ca. 100 m, *Duke 10171* (MO). Río Piñas, *Duke 10554* (MO, OS). Cuipo forests near Santa Fe, *Duke 12282* (MO). Trail from Río Pucro to Quebrada Maskia, *Duke 13069* (MO). Near helipad at Camp Hydro on Río Mortí, 229 ft, *Duke 15409* (OS). Manené to mouth of Río Cuasí, *Kirkbride & Bristan 1523* (MO, NY). ½ mi E of airstrip at El Real, *Lazor & Correa 3384* (FSU, MO, UC). Near Paya, Río Paya, *Stern et al. 236* (GH, MO, UC, US). Near El Real along trail to Río Pirre, *Stern et al. 300* (GH, MO, UC, US). Peñas Bay near hotel, *Tyson 5525* (FSU, MO), 5529 (MO). PANAMÁ: Isla del Rey, Archipelago de Las Perlas, *Correa 115* (A, DUKE). Near Jenine, Río Cañita, along Pan-Am. Hwy., *Duke 3828* (GH, MO, UC, US). Headwaters of Río Corso (off Río Pacora), ca. 500 m, *Duke 11927* (MO). Río

Pacora, just below Río Corso, *Duke 12013* (OS). San José Island, *Duke 12516* (MO). Piria-Cañasas trail near Piriá, ca. 100 m, *Duke 14325* (MO). Río Cañasas, ca. 100 m, *Duke 14522* (MO). At beginning of El Llano-Cartí Tupile road, 12 mi above Pan-Am. Hwy., 200–500 m, *Dwyer & Nee 11988* (MO). Ca. 2 mi S of Goofy Lake, *Dwyer & Stimson 8066* (DUKE, UC). Pearl Archipelago, San José Island, *Erlanson 561* (GH, NY, US); *Harlow 2* (GH, MO, US); *Johnston 1069* (GH, MO, US). 5 mi SW of Cerro Brewster, tributary of Río Chagres, ca. 1000 ft, *Lewis et al. 3382* (MO). Junction of Río Pacora and Río Corso to headwaters of Río Corso, *Oliver 2385* (MO, UC). 5 mi E of Cañita and 23 mi E of Chepo, *Tyson & Smith 4165* (MO). SAN BLAS: Hills SE of Puerto Obaldía, *Croat 16738* (MO). Ailigandí, *Dwyer 6841* (MO). Above Puerto Obaldía, *Gentry 1541* (MO).

3. **Clibadium grandifolium** Blake, Contr. U.S. Natl. Herb. 22: 599. 1924. TYPE: Costa Rica, Limón, Llanuras de Santa Clara, along Río Pacuare, 150 m, Apr 1896, *Smith 6614* (US, holotype, not seen).

C. grande Blake, Contr. U.S. Natl. Herb. 22: 601. 1924. TYPE: Costa Rica, Limón, La Florida, 80 m, 18 Jun 1897, *Pittier 11280* (GH, holotype, not seen, UC, US, photos; US, isotype).

Shrub 2–6 m tall; stems 2.5 cm diam. toward the base, glabrate to strigillose with hairs 0.3 mm long. *Leaves* broadly ovate; blades 18–32 cm long, 12–28 cm wide, acute to acuminate, the base obtuse to shortly attenuate (cordate on very large leaves), the margin serrate, the upper surface glabrate to strigillose (especially on veins) with hairs to 0.3 mm long, the lower surface moderately strigose with hairs to 0.3 mm long; petioles 5–18 cm long, to 5 mm diam., glabrate. *Inflorescence* a tightly clustered racemose panicle of 125–600 heads; peduncles 0.5 mm long. *Heads* radiate; involucre cupulate, 3–4 mm across, the bracts 8–13, ovate to obovate, 3–4 mm long, 2–2.5 mm wide, abaxially glabrate to infrequently strigillose with hairs 0.1 mm long, the upper half ciliate with hairs 0.1 mm long; paleas absent; ray florets 6–9, the corollas 2 mm long, 0.3 mm diam., the 3 lobes 0.1 mm long, the styles 2.5 mm long with branches 1.2 mm long; disc florets 7–12, the corollas 3.5–4 mm long, the throat 2.5–3 mm long and 1 mm diam., the lobes 0.6 mm long, puberulent at apex, the tube 0.3 mm diam., the anthers 2 mm long, the style 3–4 mm long, the ovary sterile, 1.5 mm long, 0.3 mm diam., villous with hairs to 1 mm long. *Achenes* 2.3 mm long, 1.8 mm diam., pubescent on the upper ⅓ with hairs 0.1 mm long; pappus absent. Chromosome number unknown.

Usually *Clibadium grandifolium* is easily recognizable by its large leaves and numerous small heads clustered together. However, in juvenile specimens, the leaves are small (e.g., *Gentry 5698*) which makes *C. grandifolium* resemble *C. asperum*. The conspicuously strigose involucral bracts of the latter species, however, provide a distinguishing character. In Panama it flowers from June to September and from December to March.

Although Blake (1924) simultaneously described both *Clibadium grandifolium* and *C. grande* as distinct species, the differences emphasized by him (numbers of florets and heads) are not sufficient to warrant formal recognition.

BOCAS DEL TORO: Santa Catalina, *Blackwell et al. 2749* (MO, UC). Chiriquicito to 5 mi S along Río Guarumo, *Lewis et al. 2082* (MO, UC). Río Changuinola near Changuinola, *Dwyer 5128* (MO). COCLÉ: Near El Valle de Antón, N rim, 800–1000 m, *Allen 224* (MO, US), *1662* (GH, MO, US), *1998* (F, GH, MO, US). El Valle de Antón, floor, 600 m, *Allen 3621* (MO). El Valle, near waterfall, *Blum et al. 2379* (MO). 2.5 mi above El Valle on road to La Mesa, *Croat 13372* (MO). Above El Valle, *D'Arcy & D'Arcy 6735* (MO); *Gentry 5698* (MO). 5 mi

N of El Valle de Antón, 1000 m, *Luteyn 1188* DUKE). 2.8 mi NW of church in El Valle de Antón, 3100 ft, *Luteyn 4059* (DUKE). Ca. 6 mi N of El Valle de Antón, *Luteyn & Kennedy 1638* (DUKE). 2 mi N of El Valle, 620–660 m, *McDaniel 8280* (US). Foot of Cerro Pilón, 2000 ft, *Porter et al. 4651* (MO, UC). DARIÉN: Cocalita near Colombian border (Pacific side), *Dwyer 5111* (US). VERAGUAS: 3–5 mi N of Santa Fe, 500–1000 m, *Gentry 3034* (MO). 5 mi W of Santa Fe, 800–1200 m, *Liesner 947* (MO).

4. **Clibadium leiocarpum** Steetz in Seem., Bot. Voy. Herald 152. 1853. TYPE: Panamá, Veraguas, volcano of Chiriquí, 7000 ft, Feb 1849, *Seemann 1592* (K, holotype, not seen, GH, US, photos).

C. schulzii Blake, Contr. U.S. Natl. Herb. 22: 602. 1924. TYPE: Costa Rica, San José, thickets at Copey, 1800 m, Mar 1898, *Tonduz 11915* (US, holotype, not seen; US, isotype).

C. leiocarpum var. *strigosum* Blake, Jour. Wash. Acad. Sci. 27: 382. 1937. TYPE: Costa Rica, San José, Cerro de Piedra Blanca, above Escasú, 31 Jan 1924, *Standley 32593* (US, holotype, not seen).

Shrub 2–4 m tall; stems 4–5 cm diam. at base, tomentose-lanate (less often villous) with hairs to 1 mm long. *Leaves* lanceolate to ovate; blades 7–19 cm long, 2–10 cm wide, acuminate, the base attenuate (less often subobtuse), the margin serrate, the upper surface strigose with hairs 0.3 mm long, the lower surface tomentose (rarely strigose) with hairs to 1 mm long; petioles 1–5.5 mm long, to 2 mm diam., tomentose-lanate (rarely strigose). *Inflorescence* a racemose panicle of 30–100 heads; peduncles 0.5–1.5 mm long. *Heads* radiate; involucre cupulate, 3–7 mm across, the bracts 7–8, narrowly to broadly ovate, 3–4.5 mm long, 1.5–4 mm wide, abaxially strigose toward the apex with hairs 0.2 mm long, the margin ciliate; paleas absent; ray florets 3–5, the corollas 1.6 mm long, 0.5 mm diam., the 3 lobes each 0.1 mm long, the styles 2 mm long with branches 0.8 mm long; disc florets 11–14, the corollas 2.7–3.3 mm long, the throat 2 mm long and 1.2 mm diam., the lobes 0.5 mm long, strigillose at apex, the tube 0.3 mm diam., the anthers 1.5 mm long, the style undivided, the ovary sterile, 2 mm long, 0.2 mm diam., apically villous with hairs to 1 mm long. *Achenes* 1.3–1.7 mm long, 1 mm diam., apically with an S-shaped neck, glabrous; pappus absent. Chromosome number unknown.

The differences in pubescence of the fertile ray ovaries as well as length of the ray corollas and sterile disc ovaries, all used by Blake (1924) to separate *Clibadium schulzii* from the earlier described *C. leiocarpum*, are not sufficient to warrant formal recognition at any rank.

Blake (1937) also recognized a variety of *C. leiocarpum*, var. *strigosum*, that included plants with strigose or accumbent-hirsute stems. Variations in the degree of pubescence do prevail in *C. leiocarpum*, and representatives of var. *strigosum* are found in Panama (e.g., *Allen 118*; *Busey 534*). However, all manner of intermediates occur between these extreme states of pubescence, and the extremes show no consistent geographical separation. Furthermore, one specimen has been found (*Allen 1341*, NY) in which the vesture is strigose on one branch and tomentose-pilose on the other (attached to the former). For these reasons, var. *strigosum* is not recognized formally in this treatment.

In Panama this species flowers from December to September.

CHIRIQUÍ: Central valley of Río Chiriquí Viejo, near "New Switzerland," 1800–2000 m, *Allen 1341* (F, GH, MO, NY, US). Near Boquete, 4500–6500 ft, *Allen 4653* (MO).

Quebrada Velo, near Finca Lerida, *Allen 4679* (MO). 20 km W of Puerto Armuelles, 400–600 m, *Busey 534* (MO). Along trail to Cerro Punta, *Croat 10478* (MO). Near Nueva Suisa, *Croat 13518* (MO). Monte Rey above Boquete, *Croat & Porter 15686* (MO). Between Cerro Punta and Bajo Grande, *Croat & Porter 16014* (MO). Above Cerro Punta, 6300 ft, *D'Arcy 5369* (MO). Nueva Suisa, Volcán District, 5700 ft, *D'Arcy 5420* (MO). Above Boquete, 4000 ft, *D'Arcy & D'Arcy 6333, 6420* (both MO). Above Cerro Punta, ca. 7000 ft, *D'Arcy & D'Arcy 6537* (MO). Río Chiriquí Viejo, opposite puebla de Cerro Punta, 7000 ft, *D'Arcy & D'Arcy 6590* (MO). Boquete district, Bajo Chorro, 6000 ft, *Davidson 141* (F, GH, MO). Volcán de Chiriquí, 7500 ft, *Davidson 954* (GH, MO, US). Valley of the Río Chiriquí Viejo N of Volcán City, 5200–5600 ft, *Duke 9036* (MO). Cerro Horqueta, ca. 1500 m, *Duke et al. 13642* (DUKE, MO). Near Boquete, 3300–4200 ft, *Lewis et al. 596* (GH, MO, UC, US). Cerro Respinga, along Boquete trail, *Gentry 5933* (MO). 1.4 mi S of Cerro Punta, 1850 m, *Graham 298* (GH). Ca. 7 mi N of El Hato de Volcán, *King 5296* (US). 4.1 mi from Boquete on road to David, *Kirkbride 94* (MO, NY). ½ mi S of Bambito, *Lazor & Correa 2696* (FSU, MO). Along road toward Cerro Horqueta, 1500–1600 m, *Luteyn 3766* (DUKE). El Boquete, 1000–1300 m, *Pittier 3136* (GH, US). Valley of the upper Río Chiriquí Viejo, near Monte Lirio, 1300–1900 m, *Seibert 245* (GH, MO, NY, US). Slopes of Volcán Barú, near Cerro Punta, 6000 ft, *Stern & Chambers 80* (MO, US). E of Boquete, Palo Alto, 5000 ft, *Stern et al. 1066* (GH, MO, UC, US), *1079* (GH, MO), *1084* (MO). Bambito, 1 mi SW of Cerro Punta, 5600 ft, *Tyson 5626* (FSU). Río Chiriquí Viejo Valley, between El Volcán and Cerro Punta, *White 5* (MO, US). Valley of upper Río Chiriquí Viejo, *White 64* (MO). Río Chiriquí Viejo Valley, near El Volcán, *White 181* (GH, MO, US). Cerro Horqueta, ca. 6 km NW of Boquete, 1700–1800 m, *Wilbur et al. 15423* (DUKE). Ca. 4 mi NW of Boquete, ca. 1350 m, *Wilbur et al. 15512* (DUKE). Halfway between Cerro Punta and Bambito, 5600 ft, *Wilbur et al. 10884* (DUKE). Ca. 6 km E of Cerro Punta, 2100–2400 m, *Wilbur et al. 15160* (DUKE). Ca. 2 km W of La Garita and 3 km WNW of Cerro Punta, 2000 m, *Wilbur et al. 15271* (DUKE). Ca. 6 mi NW of Boquete, between Bajo Quiel and Bajo Mono, ca. 1450 m, *Wilbur et al. 12008* (DUKE). Ca. 2 mi upriver from Boquete, *Wilbur et al. 17269* (DUKE). Between Cerro Punta and Las Nubes, *Wilbur & Teeri 13254* (DUKE). Between Volcán de Chiriquí and Cerro Aguacate, 6500–7200 ft, *Wilbur & Teeri 13308* (DUKE). Valley of the Río Chiriquí Viejo, E of Guadalupe, ca. 6500 ft, *Wilbur et al. 13035* (DUKE). Ca. 4 mi NW of Boquete, 4200 ft, *Wilbur et al. 13524* (DUKE). Near Casita Alta, Volcán de Chiriquí, 1500–2000 m, *Woodson et al. 908* (MO, NY, US). Near Finca Lerida, 1750 m, *Woodson & Schery 212* (GH, MO, US). Near Puerto Armuelles, 0–75 m, *Woodson & Schery 836* (MO). COCLÉ: Near El Valle, lower Río Antón, 800–1000 m, *Allen 118* (GH, MO, US).

5. **Clibadium pilonicum** Stuessy.[28] TYPE: Panamá, Coclé, mts. N of El Valle de Antón, 2500–3000 ft, cloud forest, 28 May 1967, *Lewis et al. 1745* (MO, holotype).

Arching *shrub* 3–4.5 m tall; stems at least 4 mm diam., glabrate below to densely and antrorsely strigose above with hairs 0.5 mm long. *Leaves* narrowly ovate to ovate, conspicuously 3-veined from the base; blades 8–12 cm long, 2.3–5.3 cm wide, acuminate, the base obtuse (less often shortly attenuate), the margin serrulate, both surfaces strigose with hairs 0.5 mm long; petioles 1.6–4 cm long, to 1 mm diam., strigose with hairs 0.5 mm long. *Inflorescence* a corymbose (nearly cymose) panicle with 70–86 heads; peduncles 1 mm long. *Heads* radiate; involucre funnelform, 3.5–5 mm across, the bracts 7–9, the outer two bracts ⅔ the length of the inner bracts, narrowly ovate, 3.3–4.7 mm long, 1.2–2.2 mm wide, abaxially strigose on upper half with hairs 0.2 mm long; paleas absent; ray florets 5, the corollas 1.9–2.2 mm long, 0.4 mm diam., the 2–4 lobes 0.2 mm long, the styles 2.9 mm long with branches each 1.6 mm long; disc florets 7–11, the

[28] *Clibadium pilonicum* Stuessy, sp. nov. Frutex arcuatus. Folia anguste ovata vel ovata, conspicue 3-nervata e basi. In unoquoque parte principali inflorescentiae panicula rotundata vel applanata corymbosa (prope cymosa) capitulis arcte aggregatis. Involucrum infundibuliforme. Paleae et pappus nulli.

corollas 2.9 mm long, the throat 2.2 mm long and 0.8 mm diam., the lobes 0.5 mm long, comose at apex, the tube 0.2 mm diam., the anthers 2 mm long, the style 2.5 mm long, the ovary sterile, 3.5 mm long, 0.2 mm diam., apically villous with hairs to 0.6 mm long. *Achenes* 1.8 mm long, 1.3 mm diam., apically sparingly puberulent (conspicuously pubescent on immature achenes); pappus absent at maturity (present on immature achenes as two opposing tufts of hairs 0.3 mm long). Chromosome number unknown.

In a genus so poorly known from a revisionary perspective as *Clibadium*, one hesitates to describe new species. However, after perusing nearly all original descriptions in *Clibadium*, and examining many type specimens, I have described this taxon as new.

Clibadium pilonicum differs from other species of the genus in Panama and elsewhere in having 2–4 heads tightly aggregated which are in turn secondarily clustered into tight rounded or flat-topped aggregations (*C. anceps* differs in having less tightly clustered heads). *C. pilonicum* is rare, being found only on and around the slopes of Cerro Pilón (hence the name) in Coclé Province. It flowers from May to July.

COCLÉ: Cerro Pilón near El Valle, 700–900 m, *Duke 12116* (MO, OS). Cerro Gaital Caracoral, 2700–3200 ft, *Dwyer & Correa 8844* (MO). Cerro Pilón, ca. 2700 ft, *Dwyer & Lallathin 8669* (MO).

6. **Clibadium subauriculatum** Stuessy.[29] TYPE: Panamá, Bocas del Toro, Robalo Trail, N slopes of Cerro Horqueta, 6000–7000 ft, 5–7 Aug 1947, *Allen 4970* (GH, holotype; MO, isotype).

Shrub to 2.4 m tall; stems glabrous or glabrate. *Leaves* narrowly ovate; blades 8–17 cm long, 3.6–8 cm wide, acuminate, the base subauriculate, the margin serrate, the upper surface glabrous, the lower surface strigillose with hairs 0.1–0.3 mm long; petioles 2–5 mm long, winged, the wings together 5–9 mm across. *Inflorescence* a capitate panicle with 75–104 sessile heads. *Heads* radiate; involucre cupulate, 3–4 mm across, the bracts 8–9, ovate to obovate, 3–3.4 mm long, 2–2.8 mm wide, abaxially glabrous, ciliate, the hairs 0.1 mm long; receptacle convex, 1 mm diam.; paleas absent; ray florets 5, the corollas 1.8 mm long, 0.5 mm diam., the 2 lobes 0.3 mm long, the styles 2.3 mm long with branches 1.1 mm long; disc florets 7–12, the corollas 3 mm long, the throat 2.3 mm long and 1 mm diam., the lobes 0.6 mm long, the tube 0.4 mm diam., the anthers 1.7 mm long, the style 4 mm long, the ovary sterile, 1.3 mm long, 0.3 mm diam., apically villous with hairs to 0.5 mm long. *Achenes* 1.9 mm long, 1.6 mm diam., glabrous; pappus absent. Chromosome number unknown.

This new species is similar to *Clibadium glomeratum* Greenman in having tightly clustered heads, but the former differs most conspicuously in its winged petiole tapering to a subauriculate base and in the subglabrous vesture of its stems

[29] *Clibadium subauriculatum* Stuessy, sp. nov. Frutex. Caules glabri. Folia anguste ovata, ad apicem acuminata, basi subauriculata; petioli alati, alis 5–9 mm latitudine. Inflorescentia paniculata, glomerulis unusquisque 2–5 capitulorum, arcte fasciculorum. Involucrum cupulatum. Paleae et pappus nulli.

and peduncles. *Clibadium subauriculatum* is also rare in Panama and is found only on and around Cerro Horqueta which straddles the provinces of Bocas del Toro and Chiriquí. It flowers in July and August.

CHIRIQUÍ: Near Bajo Chorro, 1900 m, *Woodson & Schery 658* (GH, MO).

7. **Clibadium surinamense** L., Mant. Pl. 294. 1771. TYPE: Surinam, exact locality and date unknown, *Alemand s.n.* (BM?, holotype, not seen).—FIG. 49.

C. villosum Benth., Pl. Hartw. 205. 1845. TYPE: Colombia, Bogotá, near the village of Tena, Feb–Apr 1843, *Hartweg 1139* (K, holotype, not seen, US, photo; G, isotype, not seen, F, US, photos).

C. lanceolatum Rusby, Descr. S. Amer. Pl. 150. 1920. TYPE: Colombia, Magdalena, Santa Marta Mts., 1898–1899, *Smith s.n.* (NY, holotype, US, photo).

Shrub, 1.7–4 m tall; stems 1–1.5 cm diam. at base, hispidulous to scabrous with hairs 0.1 mm long. *Leaves* lanceolate to ovate; blades 5–17.5 cm long, 1.5–10 cm wide, acute to acuminate, the base obtuse (sometimes shortly attenuate), the margin serrate, the upper surface weakly to moderately hispidulous with hairs 0.5 mm long, the lower surface strongly hispidulous with hairs 0.5 mm long, with veins conspicuously reticulate; petioles 3–25 mm long, to 1.5 mm diam., scabrous. *Inflorescence* a racemose (nearly spicate) panicle of 10–180 heads; peduncles 0.5–1 mm long. *Heads* radiate; involucre cupulate, 3–5 mm diam., the bracts 8–9, obovate, 3–5 mm long, 2–4.8 mm wide, abaxially strigose with hairs 0.1 mm long, the upper ⅓ of margin ciliate; paleas absent; ray florets 3–5, the corollas 2 mm long, 0.6 mm diam., the 3–4 lobes 0.5 mm long, the styles 3 mm long with branches 1.8 mm long; disc florets 11–14, the corollas 2.5 mm long, the throat 2 mm long and 1.5 mm diam., the lobes 0.6 mm long, comose at apex, the tube 0.3 mm diam., the anthers 1.8 mm long, the style 5 mm long, the ovary sterile, 2.5 mm long, 0.3 mm diam., apically villous with hairs to 0.8 mm long. *Achenes* 2.2–2.7 mm long, 1.9–2 mm diam., pubescent on the upper ⅓ with hairs 0.1 mm long; pappus absent. Chromosome number $n = 16$.

Of all the species of *Clibadium* in Panama, *C. surinamense* is the most common and has been collected in all provinces except Bocas del Toro, Los Santos, and San Blas. The most striking feature of this species is the reticulate and strongly hispidulous venation on the undersurface of the leaves. This leaf character helps distinguish *C. surinamense* from other Panamanian members of the genus. It flowers throughout the year.

Clibadium villosum, described from material collected in Colombia by Hartweg (*1139*), appears to be simply an excessively tomentose variation of *C. surinamense*. Four collections from Panama approach this extreme state of pubescence: *Allen 1016*, *Maxon & Valentine 6960*, *McDaniel 6909*, and *Woodson & Schery 731*. Critical revisionary studies are needed to determine if these variations might properly be recognized at the infraspecific level.

Although *C. surinamense* remains remarkably distinct throughout its range in Panama, several collections have been encountered that seem to intergrade into *C. asperum*, particularly in size of the heads and vesture on the undersurfaces of the leaves. These collections are: *Blum et al. 1745*, *Croat 12718*, *King 5255*, *Godfrey 2173*, and *Tyson 6315*, *6317*. All of the collections are from the vicinity

FIGURE 49. *Clibadium surinamense* L.—A. Habit (× ½). [After *Croat 10920* (F).]—B. Outer floret (× 10⅗).—C. Head (× 3⅕). [After *Rosario 38* (F).]

of Cerro Azul in the province of Panamá, except the *Croat* collection which comes from Barro Colorado Island in the Canal Zone. Both species are known to occur in the two localities. This suggests interspecific hybridization as a possible explanation for the morphological intermediacy.

CANAL ZONE: Barro Colorado Island, *Bailey & Bailey 228* (GH). Pipeline Road near Gamboa, *Clewell & Tyson 3261* (MO). Barro Colorado Island, *Croat 6243* (MO, NY, US),

6382 (MO), *10737* (F), *12584*, *12718* (both MO). Frijoles, *Croat 6267A* (F, MO, NY), *10379* (MO). Cerro Luisa, *Croat 10781* (MO). 2 mi NW of Summit Gardens, *Croat 10920* (F, MO). Forest across from Summit Golf Course, *Croat 11228* (F, MO). Between Madden Dam and Summit Naval Radio Station, *Croat 15016* (MO). Pipeline Road within 5 mi of Gamboa Gate, *D'Arcy & D'Arcy 6006*, *6194* (both MO). Behind Far Fan Beach, *D'Arcy & D'Arcy 6090* (MO). Near Coco Solo Weather Station, *Duke 4281* (MO). Toro Point, Ft. Sherman, *Duke 4325* (MO). Road C-21, *Duke 5790* (MO, UC). Gamboa, *Dwyer 2527* (FSU). Paraíso, *Dwyer 7149* (GH, MO), *7197* (MO). Madden Dam, *Dwyer & Elias 7512* (DUKE, MO, UC). Cocoli to Contractor's Hill, *Dwyer & Lallathin 8799* (MO, NY). Frijoles, *Ebinger 96*, *305* (both MO, US). Ft. San Lorenzo, *Ebinger 463* (F, MO). Coco Solo, *Elias & Kirkbride 1600* (UC). Albrook Research Forest Site, *Gallegos et al. 5140* (DUKE, FSU, MO, NY, UC). Road to Corozal, *Gervais 137* (US). Gatún Station, *Hayes 94* (GH, NY). Between Gamboa and Darién, *Heriberto 79* (F, GH, NY, US). Barro Colorado Island, *Hood 977* (F); *Kenoyer 581* (US). Ancón Hill, 100–200 m, *Killip 12103* (GH, US). Between Frijoles and Monte Lirio, 30 m, *Killip 12120* (NY, US). 20 mi S of Colón, *King 5257* (UC, US). 2 mi S of back gate to Ft. Gulick, *Lazor & Blum 5393* (FSU, MO). Monte Lirio, *Maxon 6848* (US). Near Ft. Randolph, *Maxon & Harvey 6505* (GH, US). Ft. San Lorenzo, *Maxon & Valentine 7003* (US). Gamboa, *McDaniel 5036* (FSU, MO). Empire to Mandinga, *Piper 5534* (GH, US). Near old Ft. Lorenzo, *Piper 5974* (US). Near Culebra, 50–290 m, *Pittier 2228* (GH, NY, US). Mamei Hill, 20–90 m, *Pittier 3798* (GH, US). Barro Colorado Island, *Salvoza 839* (F, GH); *Shattuck 301* (F, MO), *879* (MO); *Starry 161* (MO), *201* (F, MO). Near Summit, *Standley 25786* (MO, US). Near Ft. Randolph, *Standley 28654* (GH, US). Frijoles, *Stimson 5274* (DUKE, FSU, MO, NY, UC). Curundu, *Tyson 1040* (FSU, MO). Miraflores Locks area, *Tyson 1140* (MO, US). Chiva Chiva Trail near Miraflores Lake, *Tyson 1411* (FSU, MO). Road from Ft. Sherman to Gatún Locks, *Tyson 6286* (FSU, MO). Ca. 15 mi N of Gamboa, *Tyson 6311* (FSU, MO). 10 mi N of Gamboa, *Tyson 6312* (FSU, MO, UC). Barro Colorado Island, *Weaver & Foster 1629* (DUKE); *Wetmore & Abbe 66* (F, GH, MO), *180* (F, GH, MO). Ft. Kobe road, *Woodson et al. 1408* (GH, MO, NY). CHIRIQUÍ: Near Boquete, 900 m, *Allen 1016* (MO). 32 mi W of Santiago, *Croat 10715* (MO). Río Majugua just N of David, *D'Arcy & D'Arcy 6298* (MO). Ca. 2 mi above Concepción, ca. 1000 ft, *D'Arcy & D'Arcy 6513* (MO). Tolé, ca. 1000 ft, *Dwyer & Kirkbride 7468* (MO, UC). Río San Cristobal, 2 mi W of David, 150 ft, *Tyson 919* (FSU, MO). Near Boquete, 1200–1500 m, *Woodson & Schery 731* (GH, MO, US). Near Puerto Armuelles, 0–75 m, *Woodson & Schery 836* (GH). COCLÉ: Ca. 4 mi SE of Antón, *King 5271* (UC, US). Río Grande, *Rosario 38* (F). Llano Bonito, N of Las Margaritas, 400–500 m, *Seibert 519* (DUKE, GH, MO, NY). 3–6 km SE of El Valle de Antón, *Wilbur & Luteyn 11768* (DUKE). Between Las Margaritas and El Valle, *Woodson et al. 1743* (GH, MO, NY). COLÓN: Juan Mina Plantation, Río Chagres region above Gamboa, 25 m, *Allen 4140* (MO). Near Sardinella, *Blum & Tyson 487* (FSU, MO). Near Sabanita, *Croat 11069* (MO). Isla Grande or on mainland just opposite, *D'Arcy 4012* (MO). 1 mi N of Colón-Panamá line, *Lazor & Tyson 2983* (FSU, MO). Between France Field (Canal Zone) and Cativa1, *Standley 30344* (US). DARIÉN: Along Río Piedras, *Stern et al. 720* (GH, MO, US). HERRERA: Between Las Minas and Pesé, ca. 600 ft, *Duke 12315* (FSU, MO). Ca. 1 mi N of Las Minas and 14 mi S of Ocú, *Wilbur et al. 12078* (DUKE). Ca. 5 mi S of Ocú, *Wilbur et al. 12084* (DUKE). PANAMÁ: Hwy. toward Calzada Larga Caimito (Chilibre), *Bakes 33* (GH, DUKE, MO). Just outside Canal Zone near TTC Albrook Tower, *Blum 453* (MO). Ca. 5 mi N of Cerro Azul on road to Cerro Jefe, ca. 2400 ft, *Blum et al. 1745* (FSU, US). 3 mi above Goofy Lake near Cerro Azul, *Croat 11575* (MO). Panama City, *D'Arcy & D'Arcy 6109* (MO). On way to Cerro Azul, *D'Arcy & D'Arcy 6215* (MO). 5–6 mi E of Chepo, *Duke 4038* (GH, MO, UC, US). Panamá Viejo, *Duke 5725A* (MO). Cerro Campana, 2700–3000 ft, *Duke 8640* (MO, OS, US). Chilibre, *Dwyer 1019* (GH, MO, US). Tocumen, *Dwyer 2421* (FSU). La Campana, Cerro Campana, *Ebinger 362* (MO, US). Road to Chepo, *Garner 2* (DUKE, FSU). Sabana de Panamá, *Gervais 156* (US). Cerro Azul, 2000 ft, *Godfrey 2173* (FSU). Piña Highlands, *Hauden 102* (MO). S slopes of Cerro Azul, *King 5255* (UC, US). Chimán, *Lewis et al. 3292* (MO, UC). 10 mi N of Hwy. 1, toward Cerro Jefe, *Luteyn 1318* (DUKE). Low woods E of Bella Vista, *Maron & Valentine 6960* (GH, US). Cerro Campana, 2800 ft, *McDaniel 6909* (FSU, MO). Sabana de Panamá, *Paul 27*, *540* (both US). Villa Guadalupe, *Rivas 27* (MO, US). Cerro Azul 2000 ft, *Tyson 2173* (FSU, MO). Road from Cerro Azul to Cerro Jefe, ca. 2400 ft, *Tyson 6315*, *6317*, *6321* (all FSU, MO). Cerro Jefe, *Tyson et al. 4293* (FSU, MO). Road from Chepo to El Llano, *Tyson & Smith 4122* (FSU, MO). Cerro Campana, ca. 3000 ft, *Woods & Woods s.n.* (DUKE). Near Arraiján, ca. 15 m, *Woodson et al. 1359* (GH, MO, NY, US). VERAGUAS: San Francisco, *Dwyer 1256* (GH). Tolé, *Dwyer & Lallathin 8730* (MO). 15 mi N of Calobre, 644 m, *Luteyn 1447* (DUKE).

B. Section TRIXIDIUM

Section **Trixidium** DC., Prodr. 5: 506. 1836. TYPE: *Clibadium erosum* DC.

Paleas present; ray florets multiseriate.

8. **Clibadium pittieri** Greenman, Proc. Amer. Acad. Arts 39: 98. 1903. TYPE: Costa Rica, Limón, La Florida, 80 m, Jul 1897, *Pittier 11290* (CR, GH, syntypes, not seen).—FIG. 50.

C. pittieri f. *phrixium* Greenman, Proc. Amer. Acad. Arts 40: 38. 1904. SYNTYPES: Costa Rica, "Buissons à Tuis," 650 m, Dec 1897, *Tonduz 11479* (CR, GH, not seen, US). "Confluent du Puerto Viejo et du Sarapiqui," Jan 1893, *Biolley 7399* (CR, GH, not seen).

Shrub 1–3.5 m tall; stems antrorsely strigose to hispidulous with hairs 0.1–1 mm long. *Leaves* narrowly ovate to ovate; blades 8–19.5 cm long, 4–10 cm wide, acuminate, the base attenuate, the margin serrate, both surfaces weakly or moderately strigose to hispidulous with hairs to 0.7 mm long; petioles 1.8–7 cm long, to 1 mm diam., strigose to hispidulous with hairs to 0.5 mm long. *Inflorescence* a corymbose panicle with 8–26 heads; peduncles 1–2 mm long. *Heads* radiate; involucre cupulate, 5–6 mm across, the bracts 6–8, narrowly ovate to ovate, 2.6–3.2 mm long, 1.3–2.1 mm wide, abaxially strigose toward the apex with hairs 0.2 mm long, ciliate; paleas subtending both ray and disc florets, lanceolate, scarious, 2–3 mm long, 0.3–0.7 mm wide, on abaxial surface strigillose toward apex with hairs 0.3 mm long; ray florets 22–26, the corollas 1 mm long, 0.3 mm diam., the 4 irregular lobes 0.3 mm long, the styles 1.7 mm long with branches 0.8 mm long; disc florets 5–10, the corollas 1.6 mm long, the throat 1 mm long, 0.6 mm diam., the lobes 0.6 mm long, weakly pubescent near apex, the tube 0.3 mm diam., the anthers 1 mm long, the style 2.7 mm long, the ovary sterile, 1.7 mm long, 0.2 mm diam., pilose (especially near apex) with hairs to 0.6 mm long. *Achenes* 2 mm long, 1.8 mm diam., pubescent on upper ¼ with hairs 0.1 mm long; pappus absent. Chromosome number unknown.

Within *Clibadium pittieri*, two different types of pubescence are found on the young stems and peduncles. In some plants, the vesture is strigose (*Duke & Elias 13778*), and in others it is hispidulous (*Wilbur & Teeri 13423*). Despite this obvious difference, the populations of each type are not recognized as varieties here because no geographic separation prevails and because one collection (*Lewis et al. 975*) is clearly intermediate in these pubescence features. One could recognize these differences by describing and naming formas (as Greenman did in recognizing forma *phrixium* for the plants with hispidulous vesture), but I do not subscribe to this policy. In Panama this species flowers in all months except June to August.

BOCAS DEL TORO: Changuinola Valley, *Dunlap 283* (F, US). 10–15 mi S from mouth of Changuinola River, *Lewis et al. 975* (GH, MO, UC, US). Old Bank Island, near Chiriquí Lagoon, *von Wedel 2161* (MO). CANAL ZONE: Ca. 8.5 mi NW of Gamboa, *Wilbur & Teeri 13423* (DUKE). COLÓN: Near Guasimo on Río Miguel de la Borda, *Croat 10005* (MO). Santa Rita Ridge, *Porter et al. 4785* (MO). DARIÉN: Camp Summit, *Blackwell et al. 3667* (MO). Cerro Pirre, *Bristan 538* (MO). Near Boca Quebrada Venado, Río Tuqueza, *Bristan 1110* (OS). Cerro Pirre, *Duke 6088* (MO). Camp Summit, ca. 1200 ft, *Duke 15487* (OS). Cerro Pirre, 2500–4500 ft, *Duke & Elias 13778* (MO). Camp Summit, adjacent to Darién-San

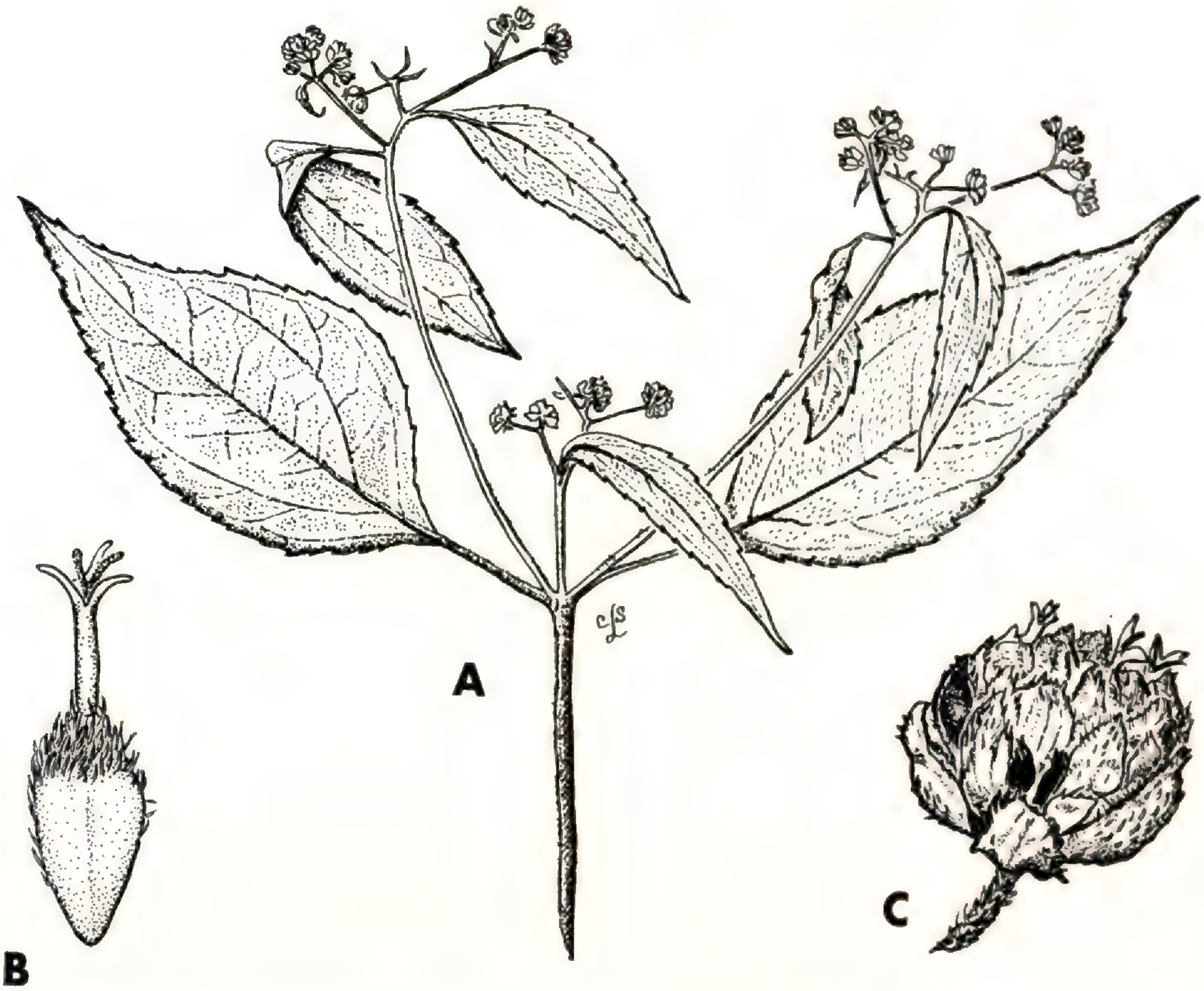


FIGURE 50. *Clibadium pittieri* Greenman—A. Habit (× 3/5).—B. Outer floret (× 11⅘).—C. Head (× 5⁹/₁₀). [After *Lewis et al. 3434* (MO).]

Blas border, 1000–1200 ft, *Oliver et al. 3667* (MO). PANAMÁ: 5 km NE of Altos de Pacora, *Busey 825* (MO). 3 mi above Interam. Hwy. on road to Cerro Campana, *Croat 12070* (MO). Cerro Campana along trail to Summit, *Croat 17175* (MO). Headwaters of Río Corso (off Río Pacora), ca. 500 m, *Duke 11918* (MO, OS). Cerro Jefe, 3100 ft, *Dwyer et al. 9496* (MO, NY). 5 mi SW of Cerro Brewster, ca. 1000 ft, *Lewis et al. 3434* (MO). E slope Cerro Jefe, 2700 ft, *Tyson 3422* (MO). VERAGUAS: 5 mi NW of Santa Fe, 700–1200 m, *Croat 23190* (MO).

50. ICHTHYOTHERE[30]

Ichthyothere Mart. in Buchn., Repert. Pharm. 35: 195. 1830. TYPE: *I. cunabi* Mart.

Herbs, subshrubs or *shrubs*; stems glabrous, scabrous or hirsute. *Leaves* opposite, sessile, or shortly petiolate, entire to subdentate. *Inflorescence* a crowded, terminal, small cymose panicle. *Heads* inconspicuously radiate, small, sessile or short-peduncled; involucre disciform, ovoid, or globose, the bracts bi- to multi-seriate, small, the inner bracts subtending and slightly adhering to ray achenes; receptacle oblong or linear; paleas broad, imbricate, subtending the disc florets; ray florets few, fertile, the corollas tubular, yellow to white, the 3–4 lobes small, the abaxial side often densely pilose in a ring, the styles bifid; disc florets perfect

[30] Generic description adapted from Bentham & Hooker (1873: vol. 2: 346).

but sterile, the corollas tubular, yellow to white, the lobes 5, the anthers 5, the style undivided, the ovary filiform, sterile. *Achenes* obovoid, thick, radially compressed, adaxially subplanar, smooth or costate, glabrous; pappus absent. Chromosome number n = ca. 33.

A genus of approximately 10 species, *Ichthyothere* is found principally in the South American tropics. At least one of the species, *I. terminalis* (Spreng.) Malme, is used as a fish poison by natives in the lower Amazon.

1. **Ichthyothere scandens** Blake, Jour. Wash. Acad. Sci. 11: 301, *fig. 1.* 1921. TYPE: Colombia, Tolima, in forest at Libano, 1100–1300 m, 26–29 Dec 1917, *Pennell 3430* (US, holotype, not seen; NY, isotype, not seen).—FIG. 51.

Slender *shrub* 1 m tall; stems at least 5 mm diam., glabrate below. *Leaves* narrowly ovate to ovate; blades 5.5–22 cm long, 2–10 cm wide, acuminate, the base attenuate, the margin denticulate, both surfaces glabrate, strigillose when young; petioles 3–50 mm long, 1 mm diam., glabrate. *Inflorescence* a cymose panicle with 10–30 heads; peduncles 1–5 mm long, becoming strigillose. *Heads* radiate; involucre cupulate, 4–5.5 mm diam., biseriate, the outer bracts 4–6, narrowly ovate to ovate, 1–1.2 mm long, 0.6–1 mm wide, abaxially glabrate, ciliate toward the apex, the inner bracts 2, conduplicate around the ray florets, obovate, glabrate, to 6 mm long and 3 mm wide, the apex rounded; paleas scarious, obovate toward the outside of the head, becoming oblanceolate within, 2–2.8 mm long, 1–2 mm wide; ray florets 2, the corollas 1.3 mm long, 0.3 mm diam., pilose on abaxial side, the styles with branches 0.8 mm long; disc florets ca. 10, the corollas yellow, 2 mm long, the throat 1 mm long and 0.7 mm diam., the lobes 0.4 mm long, the tube 0.2 mm diam., the anthers light brown, 1 mm long, the style filiform, 2 mm long with a 5-lobed nectary at the base, the ovary 0.5 mm long, 0.2 mm diam. *Achenes* with up to 10 longitudinal ridges, 4 mm long, 3 mm wide; pappus absent. Chromosome number unknown.

In Panama, *Ichthyothere scandens* can easily be distinguished from species of the related genus, *Clibadium*, by the former's few-headed inflorescence and markedly biseriate involucres. In Panama it has been collected in flower from December to March but in other areas it flowers throughout the year.

DARIÉN: Summit of Cerro Pirre, 1000–1400 m, *Gentry & Clewell 6977* (MO). Crest, Cana-Cuasi Trail, 5500 ft, *Terry & Terry 1601* (F, MO).

51. MELAMPODIUM

Melampodium L., Sp. Pl. 921. 1753; Gen. Pl., ed. 5. 392. 1754. TYPE: *M. americanum* L.

Annual *herbs* to perennial *subshrubs*; stems decumbent to erect, terete to finely striate, dichotomously branched. *Leaves* opposite, decussate, linear to ovate-rhombic, acuminate to obtuse, the base attenuate to auriculate-connate, the upper surfaces glabrous to pilose, the lower surfaces glabrous to sericeous, the margin entire to toothed. *Inflorescence* of solitary heads arising from the middle

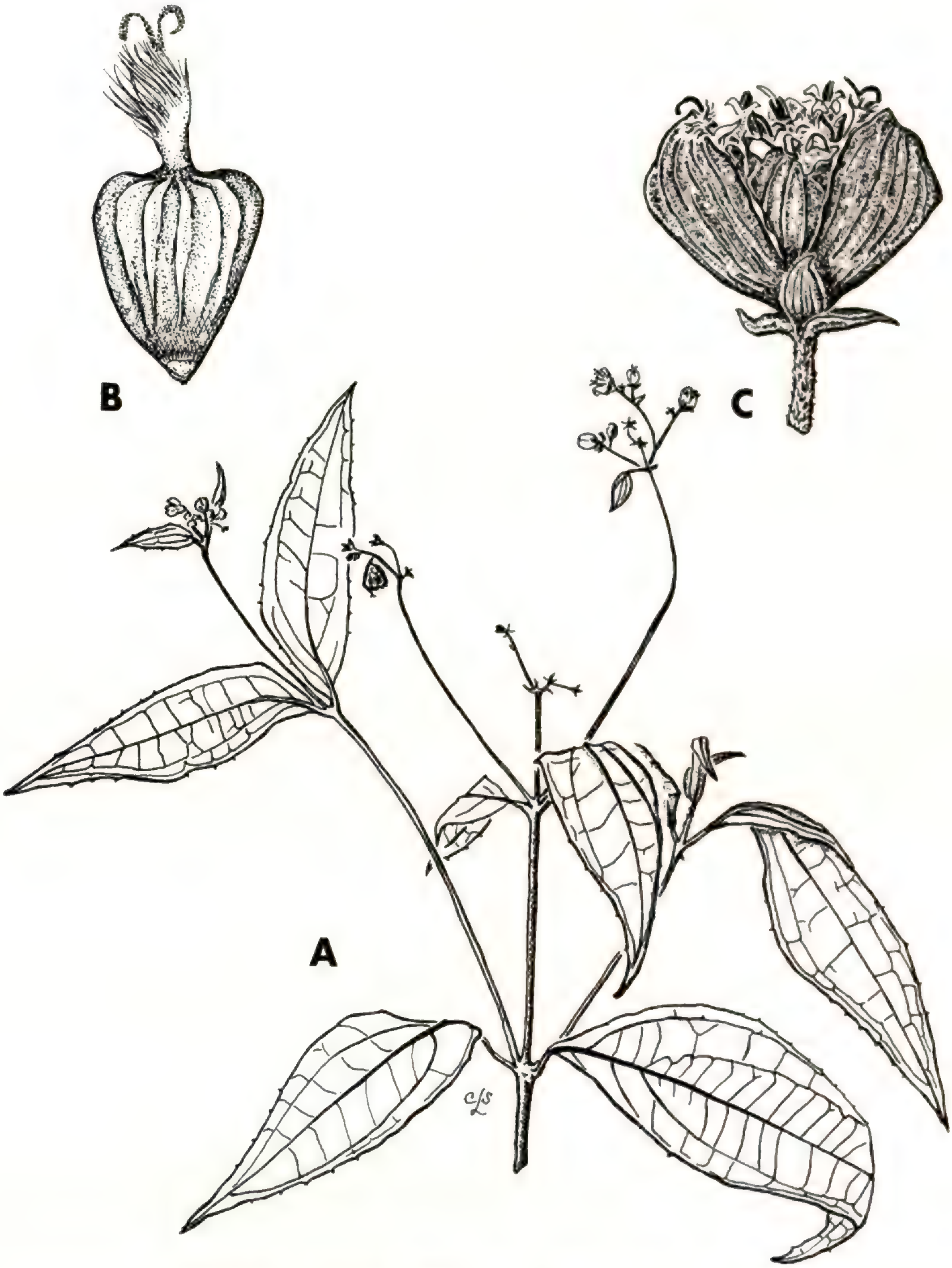


FIGURE 51. *Ichthyothere scandens* Blake.—A. Habit (× 3/5).—B. Outer floret (× 6). [After *Gentry & Clewell 6977* (MO).]—C. Head (× 6). [After *Raven 21868*, Costa Rica (F).]

and upper dichotomies; peduncles very short and stout to long and filiform. *Heads* radiate; involucre biseriate, the outer involucre spreading to cupulate, the bracts 2–5, subequal, the margins entire, separate to connate more than ⅔ their length, the adaxial surface glabrous, the inner involucral bracts each enclosing a single

ray achene (each unit termed an "involucral fruit"), often extending upward into a hood or other apical appendage; receptacle paleaceous, convex, sometimes elevated on a short cylindrical stalk 2–3 mm above the base of the outer involucre; paleas scarious, conduplicate around disc corollas; ray florets fertile, 3–13, the ligules varying shades of yellow or cream-white, bi- or tri-dentate, the tube obsolete or very short, the style branches filiform, flattened, obtuse at the apex; disc florets perfect, sterile, 3–110, the corollas yellow-green to yellow-orange, regular, 5-lobed, the throat salverform-funnelform, the anthers brown, the style linear-capillaceous, unbranched, the ovary abortive, capped by a disc; pappus absent. *Fruit* an "involucral fruit" consisting of an achene enclosed by an adnate involucral bract, the achenes asymmetrically obovoid and laterally compressed; pappus absent. Chromosome numbers $n = 9$, 10, 11, 12, 18, 20, 23, 25 ± 1, 27, 30, and 33.

This is a genus of 37 species distributed primarily in Mexico and Central America. The most important morphological feature distinguishing *Melampodium* from other genera of the Heliantheae is the fusion of the ray achenes to the inner involucral bracts, which are often ribbed and/or sculptured variously, but never spiny (as in *Acanthospermum*).

Literature:

Stuessy, T. F. 1972. Revision of the genus *Melampodium* (Compositae: Heliantheae). Rhodora 74: 1–70, 161–219.

a. Outer involucral bracts 3 (rarely 4 or 5); peduncles stipitate-glandular (B. sect. *Zarabellia*) ..... 3. *M. paniculatum*
aa. Outer involucral bracts 5; peduncles glabrous to lightly tomentose (A. sect. *Serratura*).
  b. Ligules 3.5–7 mm long ..... 2. *M. divaricatum*
  bb. Ligules less than 3 mm long ..... 1. *M. costaricense*

A. Section SERRATURA

Section **Serratura** Stuessy, Rhodora 74: 175. 1972. TYPE: *Melampodium divaricatum* (L. C. Rich.) DC.

Tap-rooted *annuals*. *Leaves* rhombic or deltoid (rarely narrowly ovate), serrate (rarely entire), petiolate. *Heads* with outer involucre cupulate or sometimes spreading, the bracts 5, the margins herbaceous; ovaries of the disc florets ovoid, less than 0.7 mm long, rudimentary. Involucral *fruits* apically nearly smooth or moderately sculptured and without a hood, or with a flattened abaxial awn. Chromosome base number $x = 12$.

1. **Melampodium costaricense** Stuessy, Brittonia 22: 118, *fig.* 7. 1970. TYPE: Costa Rica, Alajuela, Naranjo, Cerro del Espiritu Santo, 1200 m, 11 Jul 1941, *Smith* 2922 (F, holotype).

Annual *herb* 15–35 cm tall; stems erect, the lateral stems often decumbent, 0.8–3.5 mm diam., glabrous to tomentose with hairs 0.3 mm long. *Leaves* ovate-rhombic (youngest leaves approaching lanceolate), 1.5–6.5 cm long, 1.5–3.5 cm wide, acuminate to obtuse, the base obtuse-attenuate, the upper surface

infrequently strigose with hairs 0.6 mm long, the lower surface glabrous, the margin obscurely to coarsely serrate; petioles 4–23 mm long. *Inflorescence* of solitary heads; peduncles 0.5–5.1 cm long. *Heads* radiate, 4–5 mm tall, 5–8 mm across; outer involucre cupulate, 5–8 mm diam., the bracts 5, connate ¼–⅓ of their length, imbricate, ovate-orbiculate, 3–5 mm long, 2–3.6 mm wide, obtuse, the abaxial surface glabrous, the margin herbaceous, ciliate with hairs 0.3 mm long; paleas oblong-elliptic, 2 mm long, 0.7 mm wide, apically yellow, the margin erose, the midrib weak, glabrous; ray florets 5–8, the ligules yellow, elliptic, 1–1.5 mm long, 0.5–1 mm wide; disc florets 15–25, the corollas yellow, 1.1 mm diam., the throat and tube 0.5 mm long. *Fruits* 2.9–3.1 mm long, the sides with diagonal ridges and enlarged margins. Chromosome number $n = 25 \pm 1$.

Melampodium costaricense appears very similar to *M. divaricatum* in nearly all respects except that the latter species has much larger heads (8–15 mm diam.), longer ligules (3.5–7 mm long), and a chromosome number at the diploid level ($n = 12$). It flowers throughout the year.

BOCAS DEL TORO: Changuinola Valley, *Dunlap 557* (US). CHIRIQUÍ: 1 mi E of Cañas Gordas, *Croat 22320* (MO). Boquete lookout, 4000 ft, *D'Arcy & D'Arcy 6326* (MO). Above Boquete 4000 ft, *D'Arcy & D'Arcy 6340* (MO). 12 mi N of Concepción, *D'Arcy & D'Arcy 6516* (MO). 25 mi N of Concepción, *King 5290* (UC, US). Vic. of Boquete, *Lewis et al. 242* (MO), *425* (GH); *Woodson & Schery 724* (GH, MO).

2. **Melampodium divaricatum** (L. C. Rich. in Pers.) DC., Prodr. 5: 520. 1836.—FIG. 52.

Dysodium divaricatum L. C. Rich. in Pers., Syn. Pl. 2: 489, 1807, not Hort. ex DC. 1836. TYPE: Colombia, "Gairam, prope St. Martham," 1785–1789, *Richard s.n.* (P, lectotype).
Melampodium paludosum H.B.K., Nov. Gen. Sp. Pl. 4: 237. ed. qu. 1820. TYPE: Panamá, "in humidis prope ostia fluminis sinu, juxta litora Dariensis," Mar 1801, *Humboldt & Bonpland 1421* (P, holotype, not seen; P, isotype).
M. panamense Klatt, Bot. Jahrb. Syst. 8: 42. 1887. TYPE: Panamá, "ad margines silvarum," 20 Aug 1880, *Lehmann 69* (GH, holotype; G, K, US, isotypes; photo of K isotype, UC).

Annual *herbs* 15–100 cm tall; stems erect, the lateral stems sometimes decumbent and rooting at the nodes, 1–7 mm diam., glabrous to pubescent with hairs to 0.7 mm long. *Leaves* ovate to rhombic (younger leaves approaching lanceolate), 1.8–14 cm long, 0.6–8.2 cm wide, acuminate to obtuse, the base attenuate (rarely obtuse to cordate), both surfaces infrequently strigillose with hairs 0.2 mm long, the margin entire to coarsely dentate-crenate; petioles 2–25 mm long. *Inflorescence* of solitary heads; peduncles 1.5–9 cm long. *Heads* radiate, 5–8 mm tall, 8–15 mm across; outer involucre cupulate, 6–10 mm diam., the bracts 5, connate ⅓–¼ their length, imbricate, ovate-orbiculate, 3.5–6 mm long, 3–5 mm wide, obtuse, the abaxial surface glabrous to tomentose near peduncle, the margin herbaceous, tomentose near the base; paleas obovate, 2.5 mm long, 0.9 mm wide, apically yellow-orange, the margin dentate-erose, the midrib weak, glabrous; ray florets 8–13, the ligules yellow-orange, oblong-elliptic, 3.5–7 mm long, 1.6–3 mm wide; disc florets 40–70, the corollas yellow-orange, 2 mm diam., the throat 1 mm, the tube 0.5 mm long. *Fruits* 2.8–4 mm long, the sides with diagonal striations and enlarged margins. Chromosome number $n = 12$.

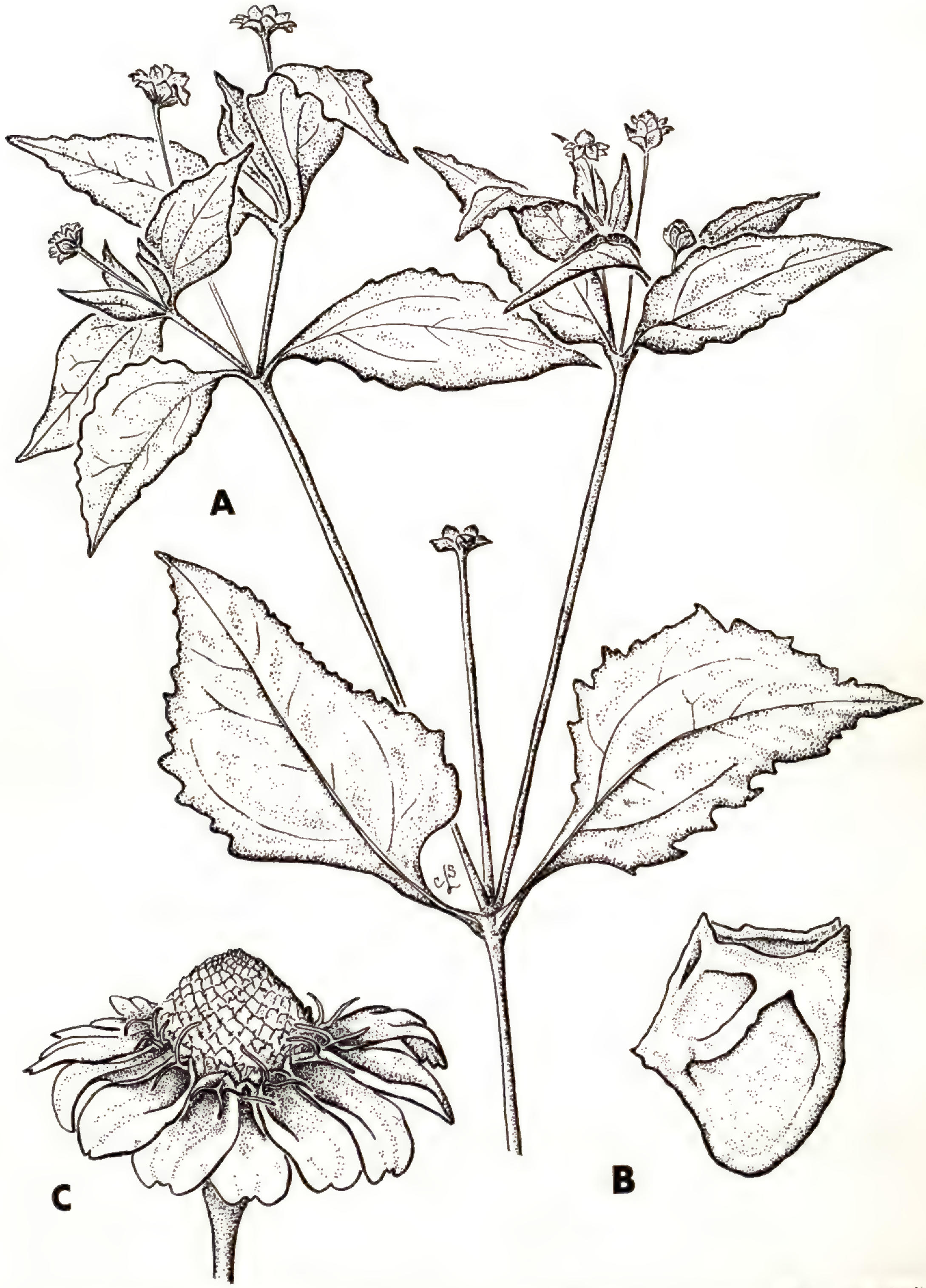


FIGURE 52. *Melampodium divaricatum* (L. C. Rich.) DC.—A. Habit (× 3/5).—B. Fruit, an achene fused with an enveloping involucral bract (× 11 3/10). [After *Stimson* 5236 (MO).]—C. Head (× 4½). [After *Stimson* 5236 (GH).]

Of all the species of *Melampodium*, *M. divaricatum* is the most widely spread, ranging abundantly throughout Mexico and Central America and even into Colombia and Brazil of South America. The ability of the seeds to germinate immediately upon dispersal, the wide ecological tolerance of the mature plants, and the ability of the stems to root adventitiously at the nodes are all factors contributing to the weedy nature of this species. This weediness is accompanied by considerable morphological variation and plasticity, especially in the height of the plants and in the size and shape of the leaves. It flowers throughout the year.

BOCAS DEL TORO: Along runway at Bocas, *Lazor et al. 2341* (FSU). CANAL ZONE: Ca. 1 mi from Gailla, *Blum 467* (FSU, MO). Vic. of Miraflores power plant, *Blum 544* (MO). Juan Mina, *Blum & Dwyer 2683* (FSU, MO). Vic. of Monkey Hill, *Cowell 27* (NY). Barro Colorado Island, *Croat 4075* (MO), *4180* (DUKE, MO, NY), *5992*, *6939* (both MO). Madden Forest, *Croat 8945* (MO). Between Madden Dam and Boy Scout Road, *Croat 8977* (MO). Pipeline Road within 5 mi of Gamboa Gate, *D'Arcy & D'Arcy 6002*, *6193* (both MO). Ft. Kobbe, *Duke 3961* (GH, US). Navy Corrosion Lab, *Duke 4436* (MO). Contractor's Hill, *Dwyer & Lallathin 8804* (MO). Frijoles, *Ebinger 76* (MO, US). Barro Colorado Island, *Ebinger 142* (MO). Ancón, *Greenman & Greenman 5002* (MO), *5043* (GH, MO), *5050* (MO). Barro Colorado Island, *Hayden 36* (MO). Gatún, *Heriberto 46* (US). Barro Colorado Island, *Kenoyer 594* (US). Ancón Hill, *Killip 3025* (NY, in part). Vic. of Frijoles, *King 5226* (UC, US). Barro Colorado Island, *Luteyn 789* (DUKE). 2 mi from front gate to Ft. Sherman, *Lazor 5379* (MO). Between Gatún and Piña, *Liesner 1330* (MO). Balboa, *MacBride & Featherstone 34* (GH, US). Monte Lirio, *Maxon 6852* (GH, US). Chiva Chiva Trail, 2 mi above Red Tank, *Maxon & Harvey 6583* (GH, US). Ft. San Lorenzo, *Maxon & Valentine 7015* (US). Balboa, *McMillan s.n.* (GH). Vic. of Corozal, *Piper 5295* (GH, US). Pedro Miguel, *Piper 5492* (US). Río Grande, near Culebra, 50–100 m, *Pittier 2106* (US). Around Gamboa, 40–80 m, *Pittier 3695* (GH, US). Between Corozal and Ancón, 10–30 m, *Pittier 6740* (US). Barro Colorado Island, *Shattuck 175* (GH). Balboa, *Standley 25658* (US). Near Gatún, *Standley 27278* (US). Near Summit, *Standley 29534* (US). Vic. of Summit, *Standley 30065* (US). Vic. of Ft. Sherman, *Standley 31225* (US). Miraflores Locks, *Stern et al. 74* (MO). K-9 road in Canal Zone at bridge, *Stern et al. 978* (GH, MO, US). Near Miraflores Locks, *Stimson 5236* (GH, MO, NY). Curundu, *Tyson 1088*, *1303* (both FSU, MO), *4192* (MO). Albrook Air Force Base, *Tyson 1102* (MO). Gatún RR station, *Tyson 3511* (FSU). 5 mi N of Cocoli, *Tyson 3875* (FSU, MO). Gamboa, *Tyson 6259* (DUKE, FSU, UC). Near Summit Golf Club, *Tyson 6621* (FSU, MO). Frijoles, *Woodworth & Vestal 725* (GH, MO). COCLÉ: El Valle de Antón, 1000–2000 ft, *Lewis et al. 2602* (MO, UC). DARIÉN: Trail between Pinogana and Yavisa, ca. 15 m, *Allen 241* (GH, MO, NY, US). Río Chico, *Burch et al. 1101* (GH, MO, NY, UC, US). Pucro to Río Pucro, *Duke 5373* (MO). Manené, *Kirkbride & Bristan 1601* (MO, NY). LOS SANTOS: 6 mi S of Las Tablas, *Croat 9720* (MO). Ca. 5 mi S of Las Tablas, *Dwyer 1226* (GH, MO). PANAMÁ: Along Río Juan Díaz above Juan Díaz, ca. 30 m, *Allen 937* (MO). 5–6 mi E of Chepo, *Duke 4039* (A, MO). San José Island, *Erlanson 365* (GH, NY, US), *500*, *594* (both GH, US). El Llano, *Gentry 2646* (MO). Cerro Jefe, ca. 1000 m, *Gentry 6759* (MO). Sabanas near Chepo, 30 m, *Hunter & Allen 64* (MO). Balboa Heights, *Killip 3025* (US) in part. 2–3 mi S of Goofy Lake, 2000–2200 ft, *Lewis et al. 280* (GH, MO, US). Sabana de Juan Corso, near Chepo, 60–80 m, *Pittier 4519* (US). Vista del Mar, *Porterfield s.n.* (NY). Arraiján, *Porterfield s.n.* (NY). Cerro Sylvestre, *Reece s.n.* (MO). Carretera Transisthmica several mi N of Chilibre, *Stimson 5074* (GH, MO). Near Arraiján, ca. 15 m, *Woodson et al. 1370* (GH, MO, NY, US).

B. Section ZARABELLIA

Section **Zarabellia** (Cass.) DC., Prodr. 5: 519. 1836.

Zarabellia Cass., Dict. Sci. Nat. 59: 240. 1829. TYPE: *Melampodium longifolium* Cerv. ex Cav.

Tap-rooted *annuals*. *Leaves* rhombic to deltoid (rarely narrowly ovate), entire to obscurely serrate, sessile or shortly petiolate. *Heads* with outer involucre usually cupulate or less often spreading, the bracts 3–5, the margins herbaceous; ovaries of the disc florets ovoid, less than 0.7 mm long, rudimentary. Involucral

fruits apically nearly smooth or moderately sculptured, or sometimes with an abaxial protuberance. Chromosome base number $x = 9$.

3. **Melampodium paniculatum** Gardn., London Jour. Bot. 7: 287. 1848. TYPE: Brazil, Goias, near Arraias, Apr 1840, *Gardner 3844* (K, holotype; F, G, NY, P, W, isotypes).

Annual *herbs*, 17–50 cm tall; stems erect, 1–3 mm diam., hispid and stipitate-glandular with hairs 0.1–1 mm long. *Leaves* ovate-rhombic (younger leaves approaching lanceolate), 1.4–5.5 cm long, 0.5–3.5 cm wide, acute to acuminate, the base attenuate, sometimes dilated almost to subauriculate, both surfaces strigose with hairs 0.3–1 mm long, the margin entire to irregularly serrate-crenate; sessile or with petioles to 5 mm long. *Inflorescence* of solitary heads; peduncles 1.4–4.2 cm long. *Heads* radiate, 2.2–4 mm tall, 3–5 mm across; outer involucre cupulate, 4–7.5 mm diam., the bracts 3, separate, ovate, 1.8–4 mm long, 1–3 mm wide, acute-acuminate, the abaxial surface strigose and stipitate-glandular with hairs 0.1–0.8 mm long, the margin herbaceous; paleas elliptical, 1.3 mm long, 0.7 mm wide, apically yellow-orange, the margin laciniate, the midrib weak, glabrous; ray florets 3–6, the ligules yellow, ovate, 1–2 mm long, 1–2 mm wide; disc florets 10–15, the corollas yellow, 1.1 mm diam., the throat and tube each 0.8 mm long. *Fruits* 2–2.8 mm long, the sides with longitudinal ribs and striations. Chromosome numbers $n = 18$ and 27.

Melampodium paniculatum is known abundantly from Costa Rica, but from only one collection in Panama. Because of the presence of this species in Costa Rica as well as in Honduras, El Salvador, Guatemala, Colombia, and Brazil, one is tempted to believe that it will some day prove to be a common element of the Panamanian flora.

CHIRIQUÍ: Valley of the upper Río Chiriquí Viejo, *White & White 111* (MO).

52. POLYMNIA[31]

Polymnia L., Sp. Pl. 926. 1753; Gen. Pl., ed. 5. 396. 1754. TYPE: *P. canadensis* L.

Erect, perennial *herbs* to *trees* more than 12 m tall; stems terete, angular or canaliculate, to 20 cm diam., the bark on large stems becoming rough. *Leaves* opposite (upper leaves sometimes subopposite); blades entire to deeply lobed, pinnately or palmately veined; sessile or petiolate, the petioles sometimes winged. *Inflorescence* of one to many heads. *Heads* radiate; involucre with bracts usually 4–6 in 1–2 series, the innermost bracts concave and at maturity partially enclosing the ray achenes, acuminate; receptacle flat or somewhat to decidedly convex; paleas usually chartaceous or infrequently of firmer texture and subulate, with or without prominent veins; ray florets in 1 or rarely 2 series, fertile, the corollas 2–3-lobed or entire, yellow, white or orange-red; disc florets perfect and sterile, the corollas yellow or sometimes purplish (when dry), the ovary sterile. *Achenes* brown, purplish-black or black, obovoid or spherical and slightly flattened laterally, sometimes 3–5-angled, the angles infrequently winged, to 7 mm long;

[31] Generic description adapted from Wells (1965).

pappus absent. Chromosome numbers $n = 14$, 15, 16, 17, ca. 20, over 25, ca. 29, 30, 33 ± 1 fragment.

This is a genus of 20 species distributed over both North and South America (Guianas excepted) in generally temperate regions. *Polymnia* can be distinguished from other genera of the Melampodiinae by its large, black fruits.

Literature:

Wells, J. R. 1965. A taxonomic study of *Polymnia* (Compositae). Brittonia 17: 144–159.

1. **Polymnia maculata** Cav., Icon. Descr. Pl. 3: 14. *tab.* 227. 1794. TYPE: "Nova-Hispania," flowering in Dec 1793 in Roy. Bot. Gard. Madrid (MA, holotype, not seen).

1a. **Polymnia maculata** Cav. var. **maculata.**—FIG. 53.

Perennial *herbs* 2.5–5 m tall; stems erect, more than 1 cm diam., glabrate below to moderately pilose above, especially on peduncles, with hairs to 1 mm long. *Leaves* ovate to deltoid, 9–45 cm long, 4–25 cm wide, attenuate, the base auriculate (rarely obtuse), the upper surface strigose with hairs 0.1–0.2 mm long, the undersurface strigose to tomentose with hairs 0.1–0.2 mm long, the margin serrate to deeply lobed or divided; sessile or with winged petioles to 14 cm long and 4 cm wide. *Inflorescence* of corymbiform cymose clusters; peduncles 2–5 cm long. *Heads* radiate, 8–11 mm tall, 1.5–2 cm across; involucre spreading, 2–3.2 cm diam., the outer bracts 5, uniseriate, separate, imbricate, narrowly ovate to ovate, 8–13 mm long, 7–11 mm wide, acute, the abaxial surface subglabrous to strigillose near the apex, ciliate with hairs 0.4 mm long, the inner bracts uniseriate, lanceolate, 4 mm long, 2 mm wide, the abaxial surface densely pilose; paleas lanceolate, 3–4 mm long, 0.4 mm wide, acuminate, the abaxial surface pilose; ray florets 8–12, the ligules yellow, elliptic, 10–19 mm long, 3–5 mm wide, the tube 1 mm long, pilose with hairs to 1 mm long; disc florets over 100, the corollas yellow, 1 mm diam., the throat 3 mm long, the tube 0.5 mm long, pilose, the anthers dark brown, the ovary sterile, 1 mm long. *Achenes* ovoid, black, 4–5 mm long, 3–5 mm diam., glabrous; pappus absent. Chromosome numbers $n = 16$, 17.

Three varieties have been recognized within *P. maculata* by Wells (1965). Neither of the other two taxa is known to occur in Panama, and both differ from var. *maculata* in conditions of vesture. Variety *glabricaulis* Blake is more glabrous throughout, and is known only from Tamaulipas, Mexico. Variety *adenotricha* Blake is more stipitate-glandular on the stems and peduncles and extends from central Mexico to Costa Rica. This species flowers primarily from June to August but occasionally the rest of the year.

CHIRIQUÍ: Ca. 1 mi SW of Boquete, 4000 ft, *Allen 4726* (GH, MO). Cerro Punta, ca. 7000 ft, *Blum et al. 2438* (FSU, MO). Boquete, *D'Arcy & D'Arcy 6505* (MO). Above Cerro Punta on slope of Cerro Respinga, 8000 ft, *D'Arcy & D'Arcy 6529* (MO). Volcán de Chiriquí, 8500 ft, *Davidson 978* (F, GH). Boquete, 6000 ft, *Ebinger 718* (F, MO). Ca. 8 mi W of David, *King 5285* (UC). Ca. 7 mi N of El Hato del Volcán, *King 5301* (UC). Ca. 1 mi S of Boquete, *King 5317* (UC). Cerro Punta, *Lazor & Correa A. 2823* (FSU). Boquete to 3 mi

FIGURE 53. *Polymnia maculata* Cav. var. *maculata*—A. Habit (× ½). [After *Allen 4726* (GH).]—B. Head (× 1$\frac{3}{10}$).—C. Outer floret with subtending involucral bract (× 3⅕). [After *D'Arcy & D'Arcy 6529* (MO).]

N, 3300–4200 ft, *Lewis et al. 633* (GH, MO, UC). Valley of the upper Río Chiriquí Viejo, near Monte Lirio, 1300–1900 m, *Seibert 292* (MO). Bambito, 1 mi SW of Cerro Punta, 5600 ft, *Tyson 5663* (FSU, MO). 2 mi S of Cerro Punta, 5600 ft, *Tyson 5943* (UC). Cerro Punta, ca. 6000 ft, *Tyson 6353* (FSU, UC), *6381* (FSU). HERRERA: ½ mi N of Macaracas on Río La Villa, *Tyson et al. 3135* (FSU, MO). LOS SANTOS: Los Toretos, *Dwyer 2419* (FSU, GH, MO).

53. UNXIA

Unxia L. f., Suppl. Pl. 56. 1781. TYPE: *U. camphorata* L. f.

Annual *herbs* to suffruticose perennials, 12–50 cm tall; stems terete, dichotomously branched. *Leaves* narrowly ovate to lanceolate, 2–10 cm long, 0.4–2.7 cm wide, acute; sessile to shortly petiolate. *Inflorescence* of one to several heads; sessile or peduncles 1–5(–10) mm long. *Heads* radiate; involucres multiseriate, the bracts free, the outermost bracts 2, ovate, acute-acuminate, opaque, the inner bracts 5–8, membranaceous, the margin scarious, obtuse-acute; receptacle convex, paleaceous; paleas lanceolate, scarious, acuminate; ray florets with ligules yellow, narrowly oblong, apically rounded, flared at base into an annular disc, the style branches filiform, flattened, obtuse; disc florets with corollas yellow-orange, regular, 5-lobed, the lobes narrowly acute, the throat narrowly funnelform, the anthers exserted from corolla ca. ½ of length, the style linear-capillaceous, undivided, the ovary sterile, pappus absent. *Achenes* ovoid, laterally compressed, narrowly keeled on adaxial and abaxial sides, notched at the point of attachment; pappus absent. Chromosome number $n = 16$.

This is a genus of 2 species in northern South America reaching into Panama. *Unxia* was regarded for over 100 years as belonging in *Melampodium*, but recent studies (Stuessy, 1969) have reestablished the genus as a close relative of *Polymnia*.

Literature:

Stuessy, T. F. 1969. Re-establishment of the genus *Unxia* (Compositae-Heliantheae). Brittonia 21: 314–321.

1. **Unxia camphorata** L.f., Suppl. Pl. 368. 1781. TYPE: Surinam, "locis arenosis," *Dalberg s.n.* (LINN, holotype, not seen, OS, photo).—FIG. 54.

U. digyna Steetz in Seem., Bot. Voy. Herald *tab. 30.* 1853; 154. 1854. TYPE: Panamá, "about Panamá," Nov. 1846, *Seemann 46* (BM, holotype, not seen; K, isotype, not seen, US, photo and fragment, F, UC, US, photos).
Melampodium camphoratum (L.f.) Baker in Mart., Fl. Bras. 6(3): 161. 1884.

Annual *herbs* or suffruticose, 12–50 cm tall; stems 0.7–2.6 mm diam., glabrous to copiously pilose with hairs to 3 mm long. *Leaves* 2–3 cm long, 0.4–2 cm wide, subentire or rarely serrate, the base obtuse or rarely attenuate, both surfaces glabrate to moderately pilose with hairs to 1 mm long. *Inflorescence* with peduncles up to 1–5(–10) mm long, 0.1–0.3 mm diam., glabrate to pilose with hairs to 1 mm long. *Heads* radiate, 3.5–6 mm tall, 6–7 mm diam. at maturity; involucral bracts 3–5 mm long, 1.5–2.5 mm wide, the inner bracts 5 or 6; receptacle 0.5 mm tall, 1 mm diam.; paleas 0.3–1.3 mm long, 0.2–0.3 mm wide, without a midrib; ray florets 3–5, the ligules 2 mm long, 0.4 mm wide, the tube 0.3 mm long, 0.2 mm diam., glabrous to strigillose with hairs up to 0.1 mm long, the style branches 0.5 mm long; disc florets 5–7, the corollas 1 mm diam., the lobes 0.5 mm long and 0.3 mm wide, the throat 1.2 mm long and 0.6 mm diam., the tube 1.2–2 mm long and 0.2 mm diam., the anthers 1 mm long, the style 2 mm long, the ovary

FIGURE 54. *Unxia camphorata* L.f.—A. Habit (× 3/5).—B. Head (× 9½).—C. Outer floret (× 12⅗). [After *Standley* 27385 (US).]

sterile, cylindrical, 0.5 mm long, 0.2 mm diam. *Achenes* 2 mm tall, 2 mm wide radially, 1 mm wide laterally. Chromosome number $n = 16$.

Although common in Colombia, Venezuela, the Guianas, and northern Brazil, the species is known in Panama from only one other collection besides the type. In other countries it flowers throughout the year.

CANAL ZONE: Corozal, *Standley* 27385 (US).

C. AMBROSIINAE[32]

TOD F. STUESSY[33]

Ambrosiinae Less., Linnaea 5: 151. 1830. "Ambrosieae." TYPE: *Ambrosia* L.

Tribe Senecioneae subtribe Ambroseae Less., Linnaea 5: 151. 1830.
Tribe Iveae Rydb., N. Amer. Fl. 33(1): 3. 1922. TYPE: *Iva* L.

54. AMBROSIA[34]

Ambrosia L., Sp. Pl. 987. 1753; Gen. Pl., ed. 5. 425. 1754. TYPE: *A. maritima* L.

Shrubs or *subshrubs* to perennial or annual *herbs*, glandular, aromatic, anemophilous. *Leaves* alternate (Panama) or opposite, unlobed to pinnately or palmately lobed or dissected, petiolate or sessile. *Inflorescence* of distinct staminate and carpellate heads normally on the same plant; staminate heads sessile to stalked, in terminal racemose or spicate clusters; carpellate heads in sessile or stalked clusters in axils of leaves subtending staminate racemes or spikes. *Heads* unisexual; staminate heads with involucral bracts laterally connate and forming a broadly funnel-shaped to cupulate or saucer-shaped involucre with the tips of the bracts more or less prominent as marginal lobes, the receptacle paleaceous, the florets several to numerous, the corollas hyaline, campanulate, 5-lobed, the stamens 5, weakly connivent, sometimes separating during pollen discharge, the appendages deltoid to long-attenuate, tails absent, the style short, truncate, penicillate, the ovary rudimentary; carpellate heads with bases of involucral bracts fused to form a hard, vase-shaped conceptacle, the bract tips forming more or less spiny processes, these straight to uncinate, flattened to terete, sometimes nearly absent, scattered over the bract surface in various patterns, the paleas absent, the florets 1–7 (if more than 1, interior of fruiting involucre compartmentalized, with each floret in a separate chamber), corolla and androecium lacking, the styles exserted through spinelike beaks at the involucral apex, elongate, linear, spreading, the ovary fertile, obovate, abruptly rounded to the short style base. Fruit an "involucral fruit" consisting of an achene tightly enclosed in the involucre. Chromosome numbers $n = 12, 17, 18, 36, 54, 72$.

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[32] Support for this investigation under NSF Grant GB-37678 is gratefully acknowledged.
[33] Department of Botany, The Ohio State University, Columbus, Ohio 43210.
[34] Generic description adapted from Payne (1964).

A genus of approximately 30 species distributed primarily in North America. Economically, *Ambrosia* is of great importance in the adverse effects caused by its wind-borne allergenic pollen. Fortunately, the genus has not yet spread to any large extent into Panama.

Literature:

Payne, W. W. 1964. A re-evaluation of the genus *Ambrosia* (Compositae). Jour. Arn. Arbor. 45: 401–438.

1. **Ambrosia cumanensis** H.B.K., Nov. Gen. Sp. Pl. 4: 276. ed. qu. 1820. TYPE: "Nova Andalusia" [Venezuela], "crescit in humidis prope Cumana," flowering in Sep, *Bonpland & Humboldt s.n.* (P, holotype, not seen).—FIG. 55.

Annual *herb* to 40 cm tall; stems erect, to 4 mm diam., sparsely villous with hairs to 1.5 mm long. *Leaves* alternate, pinnately lobed to deeply divided, 6–8.5 cm long, 2.5–4 cm wide, acute-acuminate, the base attenuate, both surfaces dotted with tiny sessile glands and strigose with hairs 0.3 mm long (approaching villous on the midrib of the undersurface), the margin deeply lobed or divided. *Inflorescence* of staminate and carpellate heads separate but on the same plant; staminate heads 30–70 with peduncles 3 mm long, in terminal elongate racemose clusters to 20 cm long; carpellate heads subsessile in axillary clusters. *Heads* unisexual; staminate heads with involucral bracts connate, forming a shallow cuplike involucre with short, irregular lobes, gland-dotted, the receptacle paleaceous with filiform paleas 1 mm long, the corollas 5-lobed, campanulate, 1.5 mm long, the throat 0.9 mm long, the stamens 5, the appendages deltoid with a mucronate tip, the styles short, truncate, the ovary rudimentary; carpellate heads with outer involucral bracts 3–5, lanceolate to narrowly ovate, to 9 mm long, gland-dotted, the inner bracts 1–3, each tightly enclosing and fused with a single ovary, the outer surface with a crown of 3–5 small spines on the upper ⅓ of the fruit, a tapering beak 0.8 mm long at the apex, corollas and androecium absent, the styles bifid with stigmatic branches to 1 mm long. *Fruits* beaked, spiny, 3–4 mm long (including beak), terete, gland-dotted. Chromosome number $n = 18$.

Ambrosia cumanensis is known in Panama from only one collection near Panama City. Because this species occurs abundantly throughout Mexico and the northern part of Central America, it is likely that the Panamanian collection represents a fairly recent introduction. The species also occurs infrequently in Nicaragua.

PANAMÁ: Near La Jagua, E of Panama City, *Bartlett & Lasser 16392* (MO).

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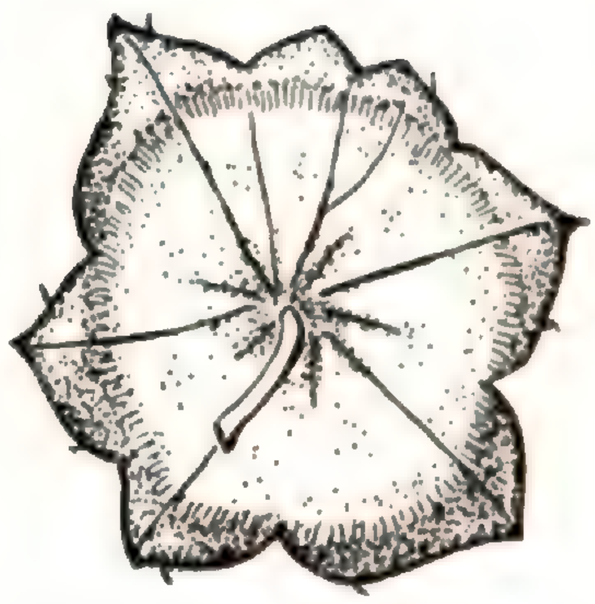
FIGURE 55. *Ambrosia cumanensis* H.B.K.—A. Habit (× 3/5).—B. Male head (× 6 3/10).—C. Involucre of male head (× 3/10).—D. Fruit consisting of achene enfolded by the involucre (× 12 3/5). [After *Bartlett & Lasser 16392* (MO).]

A

D


C

B

55. PARTHENIUM[35]

Parthenium L., Sp. Pl. 988. 1753; Gen. Pl., ed. 5. 426. 1754. LECTOTYPE: *P. hysterophorus* L.

Bitter, aromatic *herbs* or *shrubs*; stems terete to slightly ridged. *Leaves* alternate, entire to highly divided. *Inflorescence* with heads solitary or in terminal corymbs or panicles. *Heads* radiate; involucre biseriate, each series of 5 bracts; receptacle paleaceous; ray florets 5, fertile, the ligules white, the corollas and styles persistent at apex of matured achenes; disc florets perfect but sterile, all except those of the outer row falling together as a unit, the corolla tubular, 5-lobed, the anthers with white or yellow pollen. *Fruit* an "achene complex" (Rollins, 1950), the achenes obcompressed, rounded to somewhat keeled on the inner face, puberulent, the margins thickened into riblike structures which are attached to a contiguous pair of infertile disc florets and a subtending inner involucral bract, the achene and attached florets and bract falling together at maturity; pappus of 2–3 awns or scales or absent. Chromosome base numbers $x = 12$, 17 and 18.

Parthenium is a genus of 16 species distributed throughout the western hemisphere, but has the highest concentration of taxa in Mexico. Two species, *P. cinaraceum* Rollins and *P. glomeratum* Rollins, are known from as far south as Argentina.

One of the species of *Parthenium*, *P. argentatum* A. Gray ("guayule"), was cultivated in the southwestern United States as a potential alternate source of natural rubber during World War II. As a result of this economic potential, numerous investigations have been conducted upon many aspects of the species (anatomy, chemistry, etc.), and most of these publications are summarized in Hammond & Polhamus (1965).

Traditionally, *Parthenium* has been placed in the subtribe Melampodiinae. In the present treatment, however, which follows the recent suggestions of Stuessy (1973), the genus is regarded as belonging to the Ambrosiinae.

Literature:

Hammond, B. L. & L. G. Polhamus. 1965. Research on Guayule (*Parthenium argentatum*): 1942–1959. Tech. Bull. U.S.D.A. 1327: 1–157.

Rollins, R. C. 1950. The guayule rubber plant and its relatives. Contr. Gray Herb. 172: 1–72.

Stuessy, T. F. 1973. A systematic review of the subtribe Melampodiinae (Compositae, Heliantheae). Contr. Gray Herb. 203: 65–80.

1. **Parthenium hysterophorus** L., Sp. Pl. 988. 1753. TYPE: Cultivated in Hort. Uppsala, Herb. Linn. 1115.1 (LINN, holotype, not seen, IDC 177, 664: I. 5).—FIG. 56.

Annual *herb* to 50 cm tall; stems erect, much branched, to 4 mm diam., strigillose with hairs 0.3 mm long. *Leaves* lanceolate above to pinnately dissected

[35] Generic description adapted from Rollins (1950).

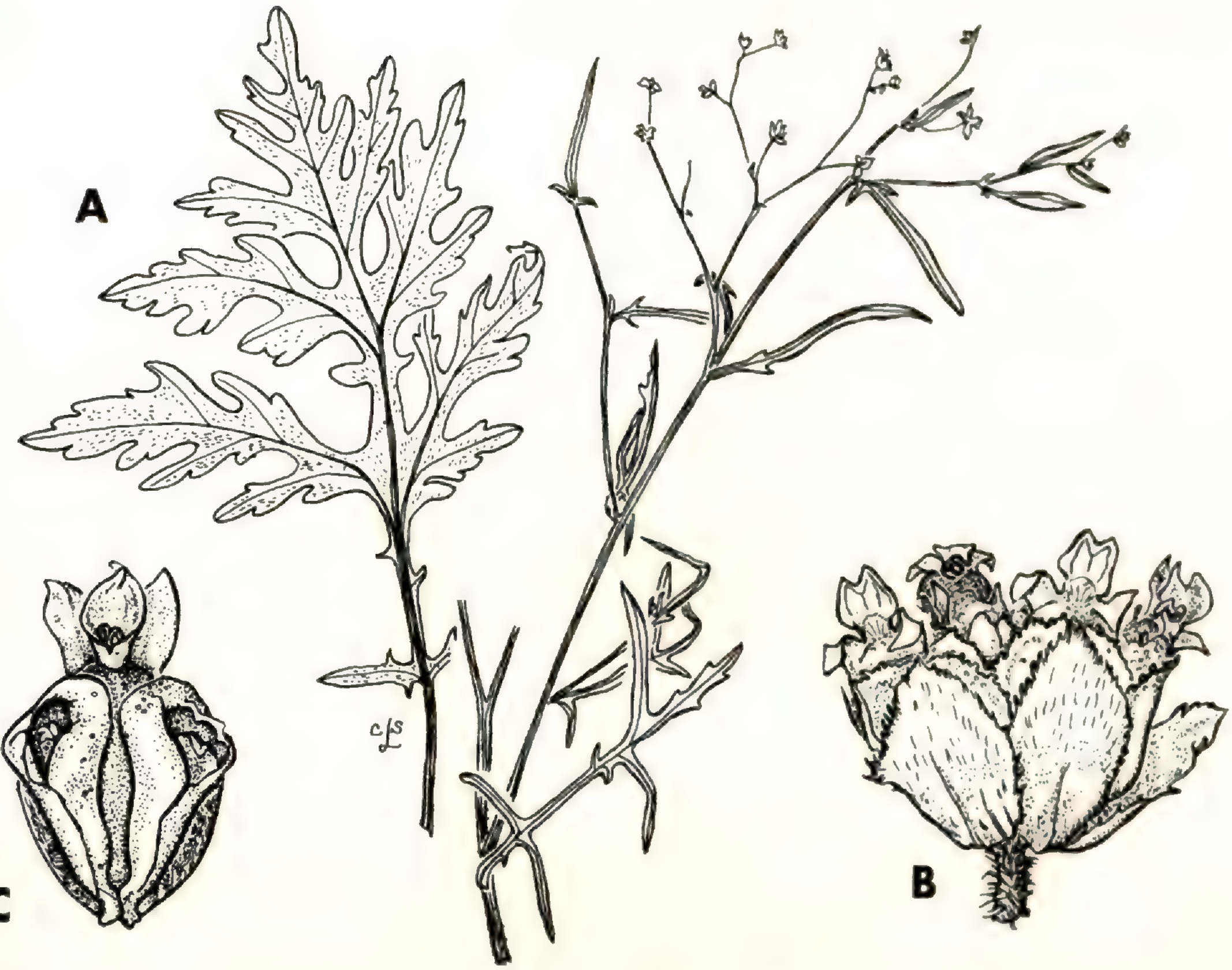


FIGURE 56. *Parthenium hysterophorus* L.—A. Habit (× ⅗).—B. Head (× 5⅒).—C. Fruit consisting of an achene, two contiguous inner florets, and an involucral bract (× 5⅒). [After *Croat 9673* (MO).]

below, 2.5–8 cm long, 0.2–4.5 cm wide, acute, the base attenuate, both surfaces strigillose with hairs 0.2–0.4 mm long, the margin entire or deeply lobed. *Inflorescence* paniculiform, of numerous small heads; peduncles 5–8 mm long. *Heads* radiate, 2.5–3 mm tall; outer involucre cupulate, 4–5 mm diam., the bracts 5, separate, narrowly ovate, 1.6–2.2 mm long, 1.5–1.8 mm wide, acute, abaxial surface strigose with hairs 0.2 mm long, the margin herbaceous, the inner bracts 5, uniseriate, each attached abaxially to the base of a ray floret, two disc paleas and two included sterile disc florets also attached to the base of the ray floret on the adaxial side (the whole unit termed an "achene complex" (Fig. 56C), each of the two disc florets and enclosing paleas is additionally attached from the base to near the apex of the achene by a thin rib); paleas elliptic, 1 mm long, 0.3 mm wide, apically fimbriate; ray florets 5, the ligules light yellow, ovate, 0.6 mm long, 0.5 mm wide, emarginate; disc florets perfect, 25–50, the corollas light yellow, narrowly funnelform, 0.3 mm diam., the throat 1 mm long, the ovary sterile, filiform, 0.7 mm long. *Achenes* flattened, 2 mm long, 1.2 mm diam.; pappus of two broad awns 0.5 mm long. Chromosome number $n = 17$.

As with the genus *Ambrosia*, *Parthenium* is known in Panama from only one collection. This specimen probably represents a recent introduction from countries

to the north such as Honduras, Guatemala, and Mexico, where the species is common. It is believed to be native to the Gulf of Mexico, including the West Indies (Rollins, 1950).

HERRERA: Near Pesé, *Croat 9673* (MO).

D. ZINNIINAE[36]

TOD F. STUESSY[37]

Zinniinae Benth. & Hook., Gen. Pl. 2: 193. 1873. TYPE: *Zinnia* L.

56. HELIOPSIS[38]

Heliopsis Pers., Syn. Pl. 2: 473. 1807. TYPE: *Buphthalmum helianthoides* L. = *Heliopsis helianthoides* (L.) Sweet.

Herbs; stems erect and ascending, or prostrate, leafy, branched, glabrous or variously pubescent. *Leaves* opposite or rarely alternate, filiform, lanceolate, orbicular, ovate, or deltoid, glabrous or variously pubescent, the margin serrate to nearly entire; nearly sessile or with petioles to 3.5 cm long. *Inflorescence* with heads terminal and from axils of upper leaves. *Heads* radiate, 0.6–3.5 cm across; involucre cupulate, the bracts 2–3-seriate, herbaceous or coriaceous, ovate-lanceolate to ovate, subequal, the outer series foliaceous and longer than the disc; receptacle broadly convex, often hollow; paleas firm, conduplicate, persisting, light brownish-yellow, red, or purple; ray florets fertile, the corollas yellow, orange-yellow, or purple, with ligules ovate-lanceolate to oblong-lanceolate, notched, persistent; disc florets perfect and fertile, the corollas yellowish, brownish-yellow or purple. Ray *achenes* triangular, the outer surface convex; disc achenes quadrangular apically, conical basally, glabrous or minutely pubescent; pappus lacking or represented by 2–3 membranaceous teeth or merely a crenulate ridge. Chromosome numbers $n = 14, 16, 28$.

This is a genus of 13 species restricted to the western hemisphere with most taxa occurring in Latin America. *Heliopsis helianthoides* (L.) Sweet is the only species confined north of Mexico.

Literature:

Fisher, T. R. 1957. Taxonomy of the genus *Heliopsis* (Compositae). Ohio Jour. Sci. 57: 171–191.

1. **Heliopsis buphthalmoides** (Jacq.) Dunal, Mém. Mus. Hist. Nat. 5: 57. 1819.—FIG. 57.

Anthemis buphthalmoides Jacq., Hort. Schoenb. 2: 13, *tab. 151*. 1797. TYPE: not seen.

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[36] Support for this investigation under NSF Grant GB-37678 is gratefully acknowledged.
[37] Department of Botany, The Ohio State University, Columbus, Ohio 43210.
[38] Generic description adapted from Fisher (1957).

Perennial *herb* to 38 cm tall; stems ascending, to 0.3 mm diam., glabrous below to sparsely pilose above with hairs to 0.5 mm long. *Leaves* narrowly ovate to ovate, 3.9–7.5 cm long, 1.9–5.4 cm wide, acute, the base obtuse to slightly attenuate, both surfaces strigillose with hairs 0.1 mm long, the margin serrate; petioles 0.5–3 cm long, 0.8 mm diam. *Inflorescence* of solitary heads; peduncles 9–14 cm long. *Heads* radiate, 7–9 mm tall, 15–20 mm across; involucre 9–13 mm diam., biseriate, the outer bracts herbaceous, narrowly ovate to elliptic, 5–6 mm long, 1.3–2 mm wide, obtuse, the abaxial surface strigillose toward the apex with hairs 0.1–0.2 mm long, the inner bracts more scarious and strigillose, but the same size and shape as the outer bracts; paleas narrowly elliptic, 4 mm long, 1.2 mm wide, obtuse, glabrous; ray florets 8–12, the ligules persistent on achene at maturity, yellow above, greenish below, narrowly elliptic, 4–6 mm long, 2.5 mm wide, the tube absent; disc florets over 50, perfect, the corollas yellow, cylindrical, 2.5 mm long, 0.8 mm diam., glabrous, the anthers 5, black. Ray and disc *achenes* similar, black, triquetrous, 3 mm long, 1.5 mm diam., glabrous; pappus absent. Chromosome numbers $n = 14$ and 28.

Perhaps the most conspicuous and distinguishing features of this species are the long peduncles with solitary heads, the ligules persistent on the ray achenes, and the involucral bracts all approximately the same length. In Panama flowering specimens have been collected in February, March, and July.

CHIRIQUÍ: Alto Lino, 4000 ft, *Maurice 878* (US). El Boquete, 1000–1300 m, *Pittier 2960* (US). Near Bajo Mona and Quebrada Chiquero, 1500 m, *Woodson & Schery 530* (GH, MO).

57. ZINNIA[39]

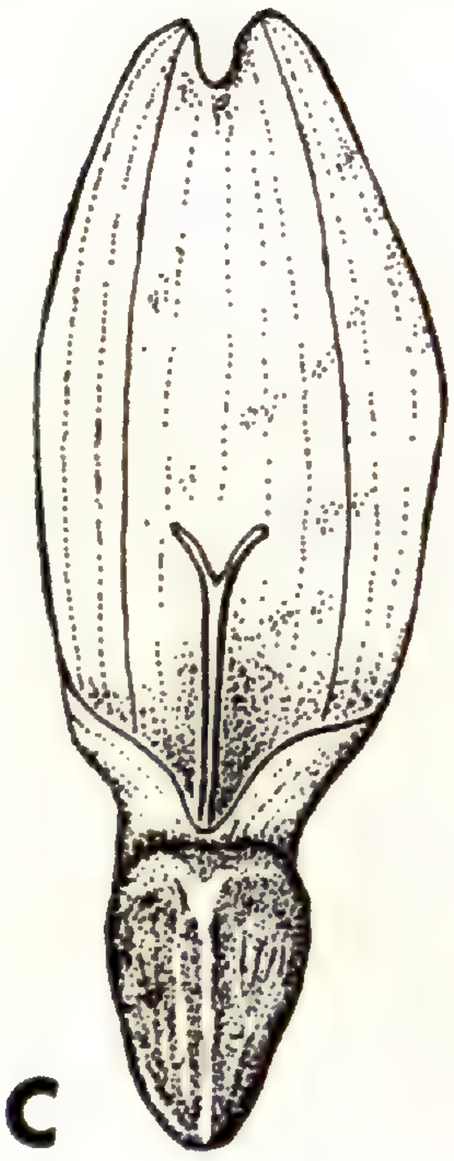
Zinnia L., Syst. Nat., ed. 10. 1221. 1759, nom. cons. TYPE: *Z. peruviana* (L.) L.

Annual or perennial *herbs* or low *shrubs*; stem angular to terete, green to sometimes purplish, smooth or striate, pubescent. *Leaves* opposite, the bases connate and sheathing the stem, both surfaces glabrous to pubescent, the margin entire; sessile or petiolate. *Inflorescence* of solitary heads; peduncles terete, striate to smooth, hollow, pubescent. *Heads* radiate; involucre cylindrical to hemispherical, the bracts multiseriate, oblong to obovate, imbricate, graduated, apically rounded and erose and/or ciliate with a dark band; receptacle slightly concave to narrowly conical; paleas persistent, conduplicate, rounded to acute, the margin erose or fimbriately lobed or entire-cuspidate, hyaline to membranaceous; ray florets fertile, the ligule usually present, persistent on the mature achene, white, yellow-orange, red, or purple, with or without a short tube, 1–3-lobed, the style bifid, filiform, acuminate; disc florets perfect, fertile, the corollas tubular, 5-lobed, sometimes zygomorphic with one lobe longer, the anthers with acute appendages, basally truncate to free-sagittate, the style bifid with filiform branches, apically acuminate and hairy or penicillately truncate. Ray *achenes* compressed to 3-angled, smooth, striate, or tuberculate, glabrous or pubescent; disc achenes compressed or angular, awned or awnless or simply bearing horns,

[39] Generic description adapted from Torres (1963).

B

A


C

C/S

glabrous or pubescent. Chromosome numbers $n = 10$, 11, $11 + 2B$, 12, 13, $19 + 2B$, 20, 21, 24, ca. 42.

Zinnia, sensu stricto, is a genus of 17 species restricted to North America with the exception of *Zinnia multiflora* which extends into Colombia, Ecuador, Peru, and Argentina. Based mainly upon experimental crossing data, Olorode & Torres (1970) recently included the related Mexican genus *Tragoceros* H.B.K., composed of 5 species, in *Zinnia* as a separate section.

Literature:

Olorode, O. & A. M. Torres. 1970. Artificial hybridization of the genera *Zinnia* (sect. *Mendezia*) and *Tragoceros* (Compositae-Zinninae). Brittonia 22: 359–369.

Torres, A. M. 1963. Taxonomy of *Zinnia*. Brittonia 15: 1–25.

1. **Zinnia elegans** Jacq., Ic. Pl. Rar. 3, *tab.* 587. 1793; 3: 15. 1795. TYPE: *Jacquin s.n.* (BM?, holotype, not seen).—FIG. 58.

Annual *herb* to 42 cm tall; stems erect to decumbent, 2–5 mm diam., glabrous below to antrorsely strigose above with hairs 0.3 mm long. *Leaves* sessile; blades narrowly ovate, 3–5 cm long, 1–2.3 cm wide, acute, the base obtuse to subauriculate, both surfaces glabrous and resin-dotted, the margin entire and ciliate with hairs 0.1 mm long. *Inflorescence* with peduncles 2–15 cm long, 2–4 mm diam. *Heads* radiate, 1.5–2.8 cm tall, 3–6 cm across; involucre hemispheric, 1.3–2.5 cm diam., multiseriate, the bracts oblong, the outermost the shortest, 2–4 mm long, 3–4 mm wide, increasing in size to the innermost, to 10 mm long, apically rounded with a green to black border, glabrous; paleas lanceolate, to 15 mm long, 5 mm wide, apically pink to purple and fimbriate; ray florets 9–12 (sometimes many more in cultivated forms), the ligules red-orange above, yellow-green below, broadly oblanceolate, 1–2.5 cm long, 0.6–1.8 cm wide, the tube absent; disc florets over 50, the corollas yellow, the lobes black-purple and densely pubescent on the abaxial surface, cylindrical, 9 mm long, 0.6 mm diam., the tube slightly swollen below throat, the anthers 5, black. Ray *achenes* triquetrous, 7–8 mm long, 4–5 mm diam., strigillose with hairs 0.1 mm long; disc achenes compressed but nearly triquetrous, with small lateral wings extending upward 0.3 mm from the apex; pappus absent. Chromosome number $n = 12$.

This species is native to Mexico, but because of its ornamental value, it has been transported to many parts of the world and has often escaped from cultivation. This is apparently what has happened to the species in Panama. Flowering Panamanian collections have been made in January, June, and August.

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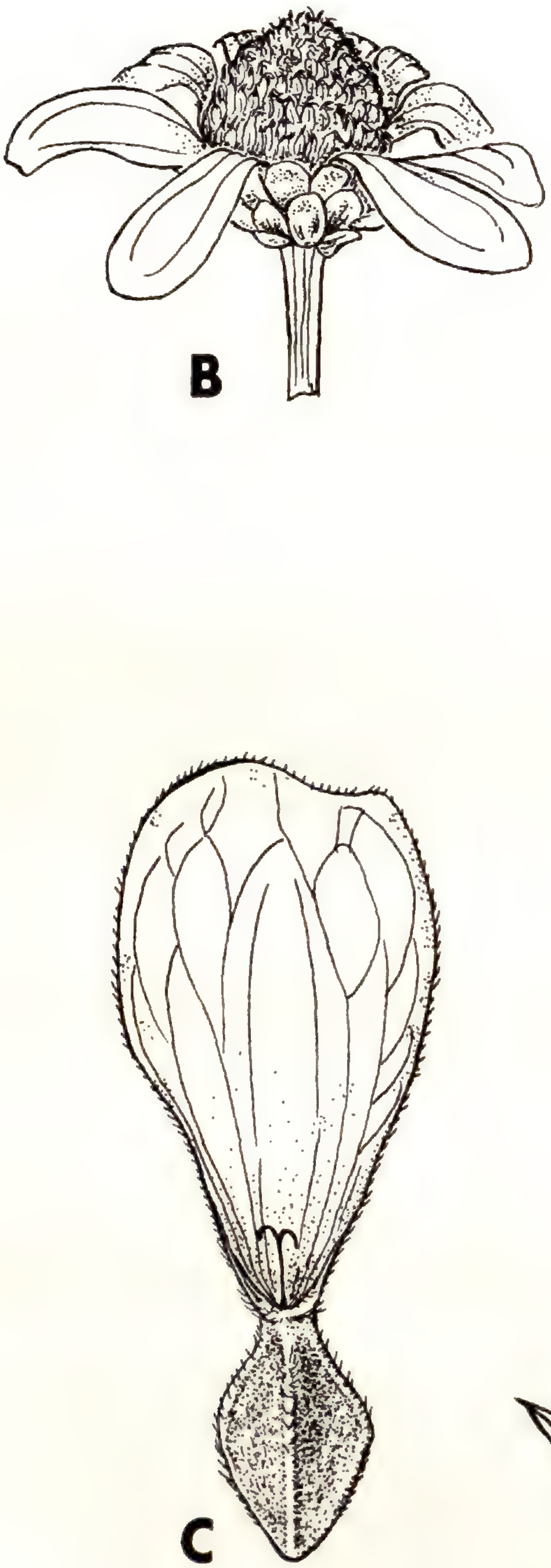
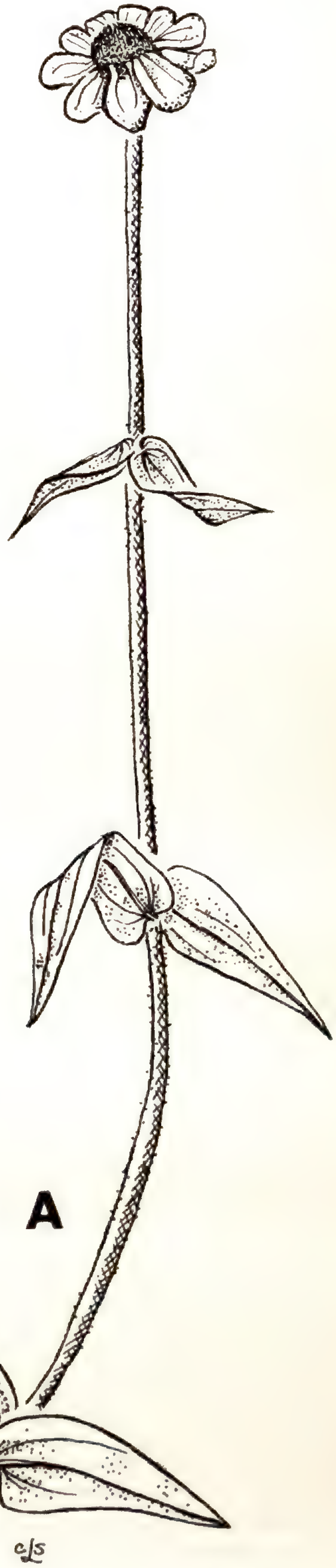
FIGURE 57. *Heliopsis buphthalmoides* (Jacq.) Dunal.—A. Habit (× 3/5).—B. Head (×1).—C. Ray floret (× 2½). [After *Pittier 2960* (US).]





cJS

CANAL ZONE: Sabanas, *Paul 7* (US). Río Pedro Miguel, near East Paraíso, *Standley 30014* (US). COLÓN: Purchased in market, Colón, *D'Arcy & D'Arcy 6700* (MO). SAN BLAS: Soskatupu, 0–150 ft, *Elias 1674* (MO, UC).

E. HELIANTHINAE

W. G. D'ARCY[40]

Helianthinae Dumort., Fl. Belg. Prodr. 71. 1827. "Heliantheae." TYPE: *Helianthus* L.

Tribe Asteroideae subtribe Ecliptinae Less., Linnaea 6: 153. 1831. "Ecliptae." TYPE: *Eclipta* L.

Tribe Helianthoideae subtribe Verbesineae Benth. in Benth. & Hook., Gen. Pl. 2: 193. 1873. TYPE: *Verbesina* L.

58. ECLIPTA

Eclipta L., Mant. Pl. 2: 157. 1771, nom. cons. TYPE CONS.: *E. alba* (L.) Hassk.

Eupatoriophalacron Miller, Gard. Dict., abr. ed. 4. 1754.

Micrelium Forsk., Fl. Aegypt. Arab. 152. 1775. TYPE: *M. tolak* Forsk.

Paleista Raf., New Fl. Bot. N. Amer. 2: 43. 1836. TYPE: *P. flexuosa* Raf. = *Eclipta alba* (L.) Hassk.

Erect or sprawling, short-lived *herbs*. *Leaves* opposite, simple, entire or toothed, mostly pubescent with verrucose hairs arising from expanded bases. *Inflorescence* solitary or a few-headed fascicle; peduncles elongate, but in our species often shorter than the leaves, appressed pubescent, especially near the apex. *Heads* radiate; involucral bracts imbricate in ca. 2 similar or irregular series, ovate to lanceolate, apically acute and mucronulate, herbaceous or somewhat indurate below; receptacle flat or somewhat convex, muricate; paleas slender, bristlelike, apically barbed; ray florets in 2–3 series, fertile, the corolla white or yellow, the tube short, puberulent, a staminode sometimes present; disc florets more numerous than the ray florets, fertile, 4-merous, the corolla campanulate, angled, the lobes ciliate, the anthers sagittate, the appendages ovate, the style branches acute. *Achene* dorsiventrally flattened, the sharp angles extended near the base, the pericarp tuberculate, brown; pappus of thick scales partially united in a cone.

Although many names have been published in the genus, there are apparently only two species, the one described here and *E. bellidioides* (Spreng.) Blake from Uruguay. *Eclipta alba* is a near-cosmopolitan weed.

[40] Missouri Botanical Garden, 2315 Tower Grove Avenue, St. Louis, Missouri 63110.

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FIGURE 58. *Zinnia elegans* Jacq.—A. Habit (× ½).—B. Head (× 1).—C. Ray floret (× 2⅘). [After *Elias 1674* (MO).]

Eclipta is distinguished by the conelike pappus, bristlelike paleas, and sagittate anthers.

1. **Eclipta alba**[41] (L.) Hassk., Pl. Jav. Rar. 528. 1848.—FIG. 59

Verbesina alba L., Sp. Pl. 902. 1753. TYPE: Herb Linn. 1020.1 ex Hort. Cliff. (LINN).
V. prostrata L., Sp. Pl. 902. 1753. TYPE: Herb Linn. 1020.4 or 1920.5 (LINN).
Eclipta punctata Jacq., Sel. Stirp. Amer. 216, *tab. 129*. 1763. TYPE: not seen.
Bellis ramosa Jacq., Enum. Pl. Carib. 23. 1769.
Eclipta erecta L., Mant. Pl. 2: 286. 1771. Based on *Verbesina alba* L.
E. prostrata (L.) L., Mant. Pl. 2: 286. 1771.
Micrelium tolak Forsk., Fl. Aegypt. Arab. 152. 1775. TYPE: Egypt, *Forskal* (BM).

Erect or sprawling ephemeral *herbs*, sometimes rooting at the lower nodes; stems sparingly pubescent, mostly below the nodes. *Leaves* opposite, simple, to ca. 7 cm long, elliptical to lanceolate, apically mucronulate, basally cuneate, the margins entire, serrate or shallowly toothed, the teeth mucronulate, pubescent and often scabridulous above and beneath with appressed, ascending, stiff, white verrucose hairs, the bases of which sometimes give the leaf a punctate appearance, eglandular, the midvein prominent, the minor venation obscure except for two ascending pinnate veins which arise partway up the lamina; petioles wanting, a ridge present at the nodes. *Inflorescence* arising terminally but often appearing axillary, a solitary head or a few-headed fascicle, the leaves near the inflorescence not reduced; pedicels slender, mostly not exceeding the leaves, sparingly pubescent, more so near the apex. *Heads* small, 3–9 mm across, radiate; involucral bracts 8–9, imbricate in 2–3 similar series, the outermost alike, ovate, acute or short acuminate, mucronulate, herbaceous or sometimes somewhat indurated below, sparingly pubescent, the venation mostly obscure but sometimes prominent in fruit; receptacle flat or convex, muricate; paleas numerous, slender, bristlelike with antrorse barbs near the apex; ray florets in 2–3 series, fertile, the corollas white, 1–2 mm long, the tube short, sparingly pubescent apically, the limb 1–2 mm long, 2-dentate, a staminode sometimes present; disc florets more numerous than the ray florets, the corolla mostly whitish, campanulate, ca. 1 mm long, the tube short, sparingly pubescent apically, the limb 4-angled, 4-lobed from ⅓–½ downward, the lobes ciliate on the ventral surface at the margin, stamens 4(?5), the anthers 0.6 mm long, basally sagittate, the appendages ovate, the style branches dorsally pubescent, acute, the nectary large, cupular, the ovary smooth, subterete. *Achene* dorsiventrally compressed and sharply angled, the angles produced into rudimentary basal wings, apically flared into a ridge subtending the pappus, the ridge with a few small hairs, pericarp tuberculate, dark brown, often withering to expose the black shiny, minutely rugose endocarp; carpopodium not evident; pappus a ring of thick, ciliate, acute, partially or completely united scales forming a cone over the top of the achene.

Eclipta alba is a cosmopolitan weed, occurring in Panama in disturbed situations in the lowlands. It flowers throughout the year.

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[41] The majority of names published in the genus *Eclipta* are synonyms here, but only the names listed have been used for Panamanian plants.

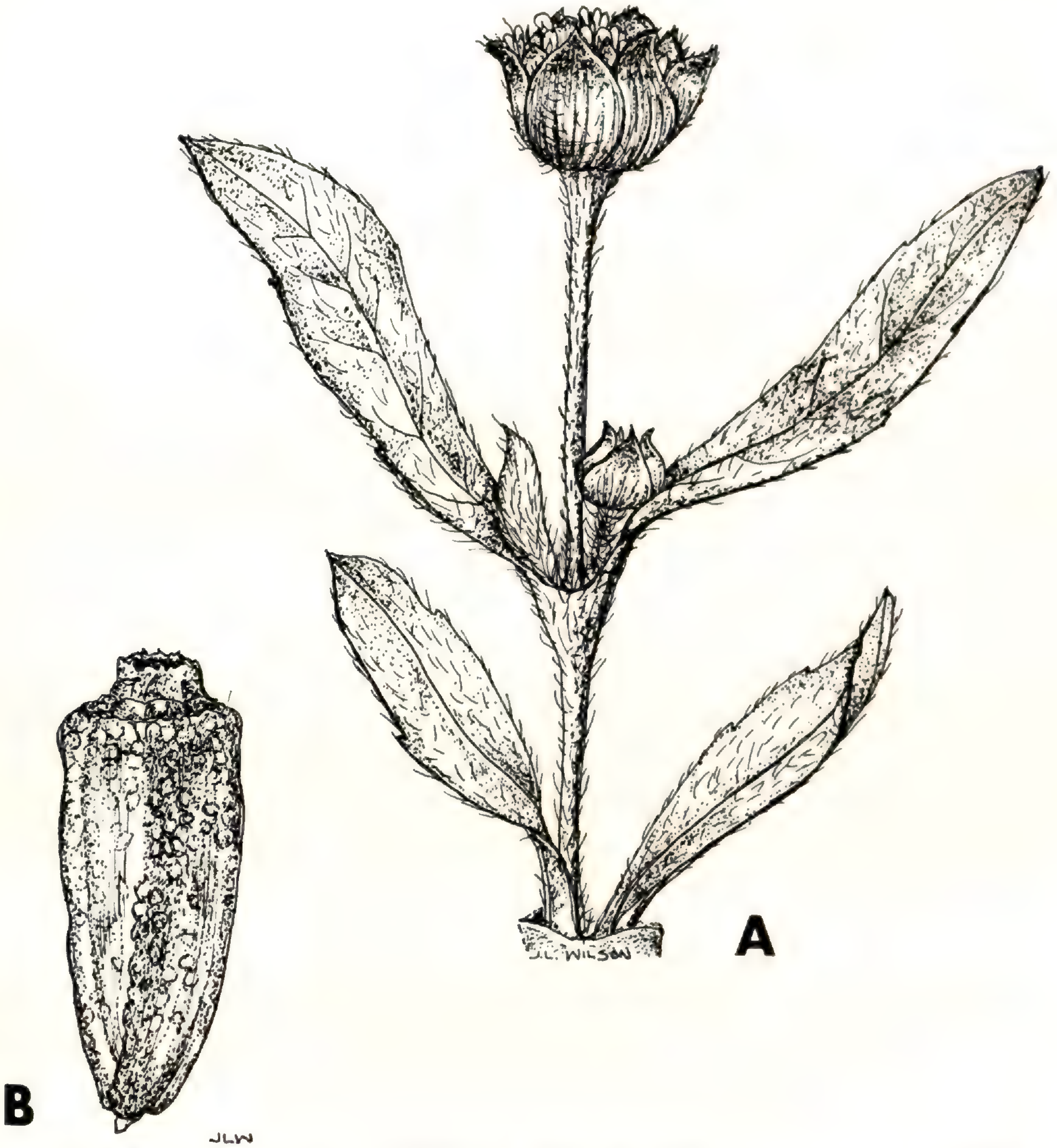

FIGURE 59. *Eclipta alba* (L.) Hassk.—A. Branch with heads (× 4⅕). [After *Robertson & Austin* 322 (MO).]—B. Achene (× 25). [After *Duke 4025* (MO).]

BOCAS DEL TORO: Railroad near station at mi 10, *Croat & Porter 16316* (MO). Railroad near station at mi 5, *Croat & Porter 16461* (MO). Almirante, *Lazor et al.* 2333 (MO). Bocas del Toro, *Lazor et al. 2356* (MO). Without locality, *Wedel 250* (MO). Old Bank Island, *Wedel 2002A* (GH, MO), *2074A* (MO). CANAL ZONE: Juan Mina, *Bartlett & Lasser 16883* (MO). 5 mi N of Gamboa, *Blum & Loftin 2309* (MO). Fort San Lorenzo, *Burch et al. 1038* (MO). Pipeline road 2½ mi from Gamboa gate, *Croat 9336* (MO). NW of Escobal, *Croat 12472* (MO). Fort Kobbe, *Duke 3960* (MO). Fort Sherman, *Duke 4377* (MO). Road K-2, *Dwyer 2891* (MO). Albrook, *Dwyer 7321A* (MO). Chagres, *Fendler 169* (MO, US). Gatún, *Heriberto 83* (GH). 1 mi N of Colón-Panamá line, *Lazor & Tyson 2990* (MO). Balboa, *Macbride & Featherstone 26* (US). Between Corozal and Panamá, *Pittier 2181* (GH, NY, US). Near Gatún, *Standley 27281* (US). Near Fort Randolph, *Standley 28751* (US). Curundu, *Tyson & Blum 2528* (MO, NY). Madden Lake, *Tyson 5507* (MO); *Woodson & Schery 960* (MO). Near Salamanca Hydrographic Station, Río Pequení, *Woodson et al. 1628* (MO, US). BARRO COLORADO ISLAND: *Croat 7957, 8271, 9562, 14817* (all MO); *Tyson 4199* (MO); *Ebinger 205*

(MO); *Shattuck 291, 599* (both MO); *Starry 221, 276* (both MO); *White 117* (MO). CHIRIQUÍ: 6 km SW of airport at Puerto Armuelles, *Busey 580* (MO). 1 mi W of Puerto Armuelles, *Croat 22034* (MO). Quebrada Caña Blanca, Burica Peninsula, *Croat 22582* (MO). Llanos Francia 4 mi from Boquete toward Dolega, 4500 ft, *Dwyer & Hayden 7611* (MO, US). From Boquete to 3 mi N, 3300–4200 ft, *Lewis et al. 425* (NY). David airport, *Lewis et al. 772* (MO). Quebrada Melliza 6 mi S of Puerto Armuelles, *Liesner 495* (MO). Quebrada Quanabanito, 2 mi SW of Puerto Armuelles, *Liesner 123* (MO). COCLÉ: Near Antón, *Woodson et al. 1702* (NY), *1709* (GH, MO). COLÓN: Colón, *Correa 1217* (MO). Near Río Lopez on Boyd-Roosevelt Hwy., *Croat 11048* (MO). Near Portobelo, *D'Arcy & D'Arcy 6683* (MO). DARIÉN: El Real, *Burch et al. 1075* (MO, US). 0–4 mi up Río Sabana from Santa Fe, *Duke 4140* (MO). Near El Real, *Stern et al. 805* (MO, US). 3 mi N of Santa Fe, *Tyson et al. 4609* (MO). 1 mi N of Sabana River, *Tyson et al. 4777* (MO). 2 mi E of Santa Fé, *Tyson et al. 4810* (MO). LOS SANTOS: Río Tonosí near Tonosí, *Lewis et al. 1576* (GH, MO, US). 5 mi SE of Chitré, *Tyson et al. 3048* (MO). PANAMÁ: Las Delicias, *Carleton 221* (NY, US). Río Pacora a 4 km del corregimiento de Pacora, *Carrera 30* (MO). Road to Cerro Azul 5 mi above Interam. Hwy., *Croat 11525* (MO). Cerro Azul, *Croat 17332* (MO). Universidad de Panamá, Panama City, *D'Arcy & D'Arcy 6110* (MO). Isla del Rey, *Duke 9573* (MO). Río Pacora below confluence with Río Corso, *Duke 11999* (MO). San José Island, *Erlanson 333* (NY, US); *Harlow 21, 51* (both US). 5 mi SW of Cerro Brewster, tributary of Río Chagres, *Lewis et al. 3378* (MO). Falls of La Chorrera, *Lewis et al. 5192* (MO). Near Tapia River, Juan Díaz region, *Maxon & Harvey 6758* (GH, US). 5 mi W of Chepo, *Tyson 6698* (MO). SAN BLAS: Río Ibedi, Mulatuppa, *Duke 8497* (MO), *8502* (MO). Isla Mosquito (Sunset Island), *Duke 8860* (MO).

59. ELEUTHERANTHERA

Eleutheranthera Poit. ex Bosc., Nouv. Dict. Hist. Nat., ed. 1., 7: 498. 1803. TYPE: not designated.

Ogiera Cass., Bull. Soc. Philom. 1818: 32. 1818. TYPE: *O. triplinervis* Cass. = *Eleutheranthera ruderalis* (Swartz) Schultz-Bip.
Fingalia Schrank, Syll. Ratisb. 1: 87. 1824. TYPE: *F. hexagona* Schrank, fide *Index Kewensis.*
Chalarium Poit. ex DC., Prof. 5: 546, pro syn., nom. nud. 1836.
Eleuthrantheron Steud., Nom. Bot., ed. 2, 1: 549. 1840, nom. nud. TYPE: Herb. Linn. 984.3.
Kegelia Schultz-Bip., Linnaea 21: 245. 1848. TYPE: *K. ruderalis* (Swartz) Schultz-Bip.

Erect or sprawling, branched *herbs*, the nodes mostly with two leaves and two branches. *Leaves* opposite, ovate, the margins entire or denticulate, 3-veined from near the base, pubescent with verrucose hairs having expanded bases, and mostly copiously glandular beneath; petiole slender. *Inflorescence* a terminal aggregate of 1–several heads; peduncles slender, ebracteate and ebracteolate. *Heads* inconspicuous, discoid, the involucral bracts loosely imbricate in 2–3 series, herbaceous, the innermost sometimes paleaceous and partly enfolding the florets; receptacle minute, ill-defined; paleas mostly flattened, slightly exceeding the achenes; florets 5-merous, the corolla lobes ventrally pilose, the anthers apically free with rudimentary appendages, basally auriculate, the style branches lanceolate, the ovary laterally flattened, 3-angled, minutely puberulent. *Achene* brown, clavate, indistinctly angled, tuberculate, contracted below an apical peg, the shoulders sometimes sparingly pilose.

Eleutheranthera embraces the pantropical weed, *E. ruderalis*, and a second species reported from Madagascar.

The inner involucral bracts, so-called because they are the last series of bracts external to the florets, are in fact the outer series of paleas, the ray florets peripheral to them having been lost through reduction. Thus the innermost involucral bracts represent in this case a homologous inner system of paleas and

the green, herbaceous bracts represent an involucral system of bracts. The apex of the achene in *Eleutheranthera* resembles a peg, sometimes pubescent, which is formed by an abrupt contraction of the achene body above the locule, and coherence to the slightly shorter nectary.

1. **Eleutheranthera ruderalis** (Swartz) Schultz-Bip., Bot. Zeitung (Berlin) 24: 165. 1866.—FIG. 60.

Melampodium ?ruderale Swartz, Fl. Ind. Occ. 3: 1372. 1806. TYPE: Jamaica, *Swartz* (? BM, not seen).
Eleutheranthera ovata Poit. ex Steud., Nom. Bot., ed. 2, 1: 549. 1840, nom. nud.
Kegelia ruderalis (Swartz) Schultz-Bip., Linnaea 21: 245. 1848. TYPE: not seen.
K. ramossisima Schultz-Bip., Linnaea 21: 245. 1848. Provisional name for *K. ruderalis* (Swartz) Schultz-Bip.
Eleutheranthera prostrata Schultz-Bip., Bot. Zeitung (Berlin) 24: 239. 1866. TYPE: not seen.

Erect or sprawling *herbs* to 30 cm tall; stems glabrate to pilose. *Leaves* opposite, ovate, mostly 3(–8 mm) long, apically acute or acuminate, basally obtuse, acute or acuminate, the margins entire or crenulate-dentate, 3-veined from near the base, both sides pubescent with verrucose hairs and glandular; petiole slender, less than ⅓ the length of the leaf. *Inflorescence* a terminal aggregate of 2–5 heads, the subtending leaves not reduced; pedicels slender, pilose, often longer than the head. *Heads* discoid, 4–6 mm long; involucral bracts in two series of 4–5 each, the outermost slightly imbricate, ovate, apically acuminate or acute, often mucronulate, green, ciliate, dorsally pubescent on the lower portion, ventrally on the apical portion with copious sessile glandular excrecences, the midvein impressed ventrally, slightly elevated dorsally, with two inconspicuous veins running parallel and close to the margin, some of them exceeding the flowers, the innermost receptacular or paleaceous, folded from the costa to partially enclose the florets, apically green, acuminate, ciliate; florets 2–6, 4–5 mm long, somewhat arched, the corolla 2.5 mm long, campanulate, the tube short, the limb apically 5-lobed, the lobes ventrally pilose, yellow, basally hardly expanded, the stamens 5, the anthers black, the upper ¼ free, the appendages rudimentary, the anther collar thickened, prominent, the anthers basally auriculate, the adjacent auricles mostly connate, the style branches lanceolate, conspicuously dorsally pubescent, the stigmatic surface confined to two lateral ridges on the lower ¾, the apical ¼ flattened and thinner, the nectary coroniform, 0.25 mm long, the ovary laterally flattened, 3-angled, evenly and finely puberulent, contracted above the locule and expanded into a pilose, coroniform pappus not exceeding the nectary. *Achene* 3 mm long, brown, the pericarp buff colored, prominently tuberculate, especially along the ribs and near the apex with dark brown umbonate tubercules, sparingly pubescent with weak spreading white hairs; pappus an apical peg, dark brown and white-pubescent on top.

Eleutheranthera ruderalis is a plant of the lowlands, occurring in disturbed spots in sun or shade.

Sometimes mistaken for *Eclipta*, to which it is closely related, or with *Synedrella*, *Eleutheranthera* is distinct in its glandular foliage, discoid heads, and loosely arranged involucral bracts. The florets are quite inconspicuous but the

FIGURE 60. *Eleutheranthera ruderalis* (Swartz) Schultz-Bip.—A. Habit (× ½). [After *Croat 6347* (MO).]—B. Head (× 4⅘). [After *Croat 7057* (MO).]

fruits and empty bracts are usually more readily observed. *Eleutheranthera* is similar in appearance to *Wedelia keatingii* which has larger leaves, larger bracts, and winged, flattened achenes.

BOCAS DEL TORO: Near Changuinola, *Croat & Porter 16486* (MO). Lower Changuinola, *Stork 274* (US). CANAL ZONE: Tropic Test Centre Miraflores Annex, *Blum 681* (MO). Barro Colorado Island, *Croat 6347* (MO). Summit Garden, *Croat 10289* (MO). Road to Gamboa airport, *Croat 14605* (MO). Road K-10D near divide W of canal, *Croat 15134* (MO). Farfan

Beach, *D'Arcy & D'Arcy 6069* (MO). Sosa Hill, *Duke 4661* (MO). Miraflores, *Dwyer 1009* (MO). Fort Clayton, *Dwyer 1051* (MO). Gatún, *Hayes 676* (NY). Near Frijoles, *King 5228* (US). Miraflores Locks, *Stern et al. 77* (MO, US). Curundu, *Tyson 1080, 1085, 6642* (all MO). Albrook Air Force Base, *Tyson 1101* (MO). Miraflores locks area, *Tyson 1256* (MO). Fort Sherman, *Tyson & Blum 3775* (MO). Macapale Island in Madden Lake, *Tyson 5481* (MO). Near Miraflores Lake, *White 173* (MO). Near Salamanca Hydrographic Station, Río Pequeni, *Woodson et al. 1612* (MO, NY). CHIRIQUÍ: Quebrada Tuco, 9 mi S of Puerto Armuelles, *Liesner 169* (MO). COCLÉ: Río Hato Airstrip, *Blum & Dwyer 2483* (MO). DARIÉN: Manené to mouth of Río Cuasí, *Kirkbride & Bristan 1499a* (MO, NY). PANAMÁ: Las Delicias, *Carleton 47* (US). Ca. 1 mi N of Panam. Hwy. on road from El Llano, *D'Arcy & D'Arcy 6127* (MO). Hills NE of Hacienda La Joya, 50–300 m, *Dodge et al. 16878* (MO). Near Jenine, Río Cañita, *Duke 3811* (MO). Nueva Gorgona, *Duke 4527* (MO). Near Goofy Lake, Cerro Azul, *Ebinger 985* (MO). San José Island, *Erlanson 360, 595* (both US). 7 mi W of Chepo, *Gentry & Tyson 1634* (MO). San José Island, *Johnston 890* (US). Ca. 13 mi SE of La Chorrera, *King 5260* (US). Road to Cerro Jefe, *Lewis et al. 227* (US). Río Chilibre, *Piper 5663* (US). Matías Hernández, *Pittier 6752* (NY, US). Taboga Island, *Standley 27032* (US). Near Las Sabanas, *Standley 40783* (US). Saboga Island, Pearl Islands, *Tyson 5590* (MO). SAN BLAS: Permé, *Cooper 272* (NY, US). Río Ibedi, Mulatuppa, *Duke 8507* (MO).

60. GARCILASSA

Garcilassa Poepp. & Endlich., Nov. Gen. Sp. Pl. 3: 45, *tab. 251.* 1843. TYPE: *G. rivularis* Poepp. & Endlich.

Erect, branching, sparingly pubescent *herbs*; branches slender; roots fibrous. *Leaves* alternate but sometimes appearing opposite, simple, ovate, the margins serrate, chartaceous, sparingly pubescent; petioles slender. *Inflorescences* several, loose, small, umbellate or cymose panicles subtended by foliaceous bracts; pedicels slender, subtended by minute linear bracteoles. *Heads* small with few florets, discoid; involucral bracts 3–5, ovate-lanceolate, unequal, pubescent, drying reddish brown; receptacle minute; paleas indurate, acute, longer than the involucral bracts, pubescent, enveloping the florets; disc florets 3–5, the corolla narrowly campanulate, pubescent outside, the anthers black with narrowly deltoid appendages, basal auricles present but obscured, the style branches deltoid with a cuspidate apex, pubescent, the style base expanded, slightly immersed in the nectary, the ovary compressed. *Achene* plump, pubescent without longitudinal veins; pappus a ring of minute, partially connate scales.

This genus is superficially similar to *Stevia* in its reduced heads, but the florets, individually wrapped in paleas, and the pappus of minute scales easily separate the two genera, which are in fact, only distantly related. Superficially the plants are similar to those of *Eleutheranthera ruderalis* but the flower structure and achene is quite different, and the pubescence is sparser.

1. **Garcilassa rivularis** Poepp. & Endlich., Nov. Gen. Sp. Pl. 3: 45, *tab. 251.* 1843. TYPE: Peru, *Poeppig 1459* (B, if extant, US, photo).—FIG. 61.

Erect *herb* to 1.3 m tall; stems slender, drying striate, puberulent with sparse, short hairs, lower nodes sometimes with a distinct intrapetiolar line; roots short and fibrous. *Leaves* alternate but sometimes appearing opposite, ovate, to 10 cm long, apically acuminate, basally obtuse, the margins serrate, 3 principal veins diverging from just above the base, chartaceous, sparingly pubescent on each side; petiole slender, to 1.5 cm long. *Inflorescences* several, terminal or on short

shoots below the apex, umbellate or weakly cymose paniculate aggregates of 3–12 heads; peduncles slender, puberulent, flexuous, to 3 cm long, foliaceous bracts often present; pedicels slender, mostly shorter than the heads, bracteoles pubescent, linear, scalelike. *Heads* small with few florets, discoid; involucral bracts 3–5, ovate-lanceolate, dorsally pubescent, unequal, to ca. 3 mm long; receptacle minute; paleas indurate, enveloping the florets, ca. 5 mm long, apically out-curving, acute, sometimes short-cuspidate, pubescent; florets 3–4, ca. 5 mm long, the corolla narrowly campanulate, ca. 3 mm long, pubescent outside with appressed, ascending white hairs, the 5 lobes narrowly deltoid, the anthers black, ca. 1.2 mm long, the appendages narrowly deltoid, black at least in part, the basal auricles obscured by a thickening of the filament apex which gives the anther a truncate appearance, the style branches recurved, flattened-deltoid with a short-cuspidate apex, pubescent inside and out, the dorsal surface of the area just below the dichotomy black, the style base expanded-ellipsoid, basally truncate but slightly immersed in the short, cylindrical nectary, the ovary compressed. *Achene* brown, 3 mm long, only slightly flattened, not veined, reddish brown, evenly pubescent with numerous, short, ascending hairs, the bases of which appear glandular; pappus a ring of minute scales.

This species may be recognized by its small heads of few, palea-enclosed florets and by the plump, pubescent achenes which lack longitudinal veins. Collector's notes record flower color as greenish yellow, green or greenish, but in dried condition, the corolla and the dorsal surface of the style branches appear blackish.

The species ranges from Costa Rica to Peru and Bolivia.

BOCAS DEL TORO: Río Teribé, near Quebrada Lukulon, *Kirkbride & Duke 518* (MO). Río Cricamola, 10–50 m, *Woodson et al. 1821* (MO). CANAL ZONE: Between Frijoles and Monte Lirio, *Killip 12163* (NY, US). CHIRIQUÍ: 1 mi E of Cañas Gordas near Costa Rican border on road to Volcán, *Croat 22343* (MO). DARIÉN: Caña vic., 2000–6500 ft, *Williams 955* (NY, US). PANAMÁ: Confluence of Río Pacora and Río Corso, ca. 450 m, *Duke 11966* (MO). Junction of Río Pacora to headwaters of Río Corso, *Oliver 2372* (MO).

61. LASIANTHAEA

Lasianthaea DC., Prodr. 5: 607. 1836, new name for *Lasianthus* Zucc., ined., not *Lasianthus* Adans. 1763, nom. reiic. = *Gordonia* Ellis. 1771 (Theaceae), nor Jack. 1823 (Rubiaceae). TYPE: *L. helianthoides* Zucc. ex DC.

Zexmenia A. Gray, Pl. Wright. 1: 113. 1852, not *Zexmenia* LaLlave 1824. TYPE: *Lasianthaea helianthoides* Zucc. ex DC.

Perennial *herbs*, *shrubs*, or *trees*, mostly pubescent; stems slender, striate. *Leaves* opposite, simple, ovate or elliptical, serrate, pinnate or 3-veined, mostly with an intrapetiolar ridge. *Inflorescences* paniculate or umbellate, rarely solitary heads, bracts mostly present. *Heads* radiate; involucre of oblong, basally imbricate nonrecurving bracts in 2 or more series, alike in shape but not in size; paleas scarious, enfolding the florets; ray florets few, yellow (Panama), narrow, apically notched, the style branches flat, the ovary fertile, strongly trigonous; disc florets numerous, the tube forming ca. ¼ the corolla length, the throat tubular, the 5 lobes puberulent, the stamens with deltoid appendages and the auricles obscured by a

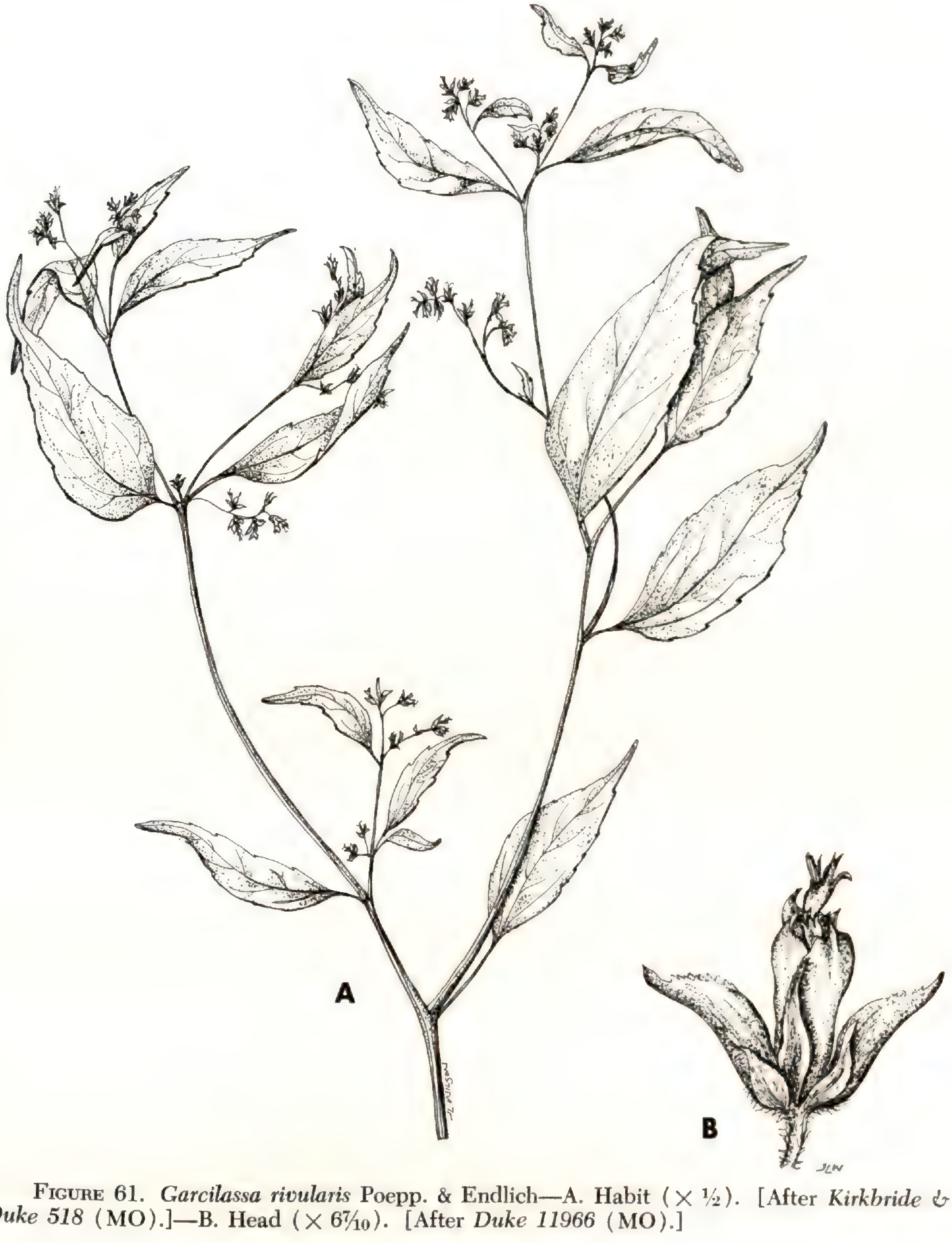

FIGURE 61. *Garcilassa rivularis* Poepp. & Endlich—A. Habit (× ½). [After *Kirkbride & Duke 518* (MO).]—B. Head (× 6⁷⁄₁₀). [After *Duke 11966* (MO).]

truncate expansion of the filament apex, the style branches lanceolate, pilose, the style base immersed in a cylindrical nectary, the ovary fertile, flat, thin-winged. *Achenes* shiny, sharply 2–3-angled, 2–3-awned; awns inserted at the apical margin of the achene with narrow dorsal wings near the point of insertion, united by a ring of fused squamellae.

This genus differs from the similar genus *Zexmenia* in several respects. The leaves are all opposite, the outermost involucral bracts are alike and mostly

compact and not bending outwards, the achenes are not winged when mature except in the region of pappus insertion, and the straight awns are inserted near the edge of the achene apex rather than inwards and bent out and then upwards as in *Zexmenia*.

The name *Zexmenia* has been used to embrace two distinct genera, and recognition of the distinction results in resurrection of the name *Lasianthaea* for the species known from Panama. *Zexmenia* LaLlave & Lexarza was long interpreted as based on elements of *Lasianthaea*, but examination of the type of *Z. serrata* LaLlave & Lexarza by Blake (1930: 254–255) showed it to typify a taxon different from *Lasianthaea*. A proposal to conserve *Zexmenia* A. Gray over *Zexmenia* LaLlave & Lexarza (Becker, 1972) was rejected. *Lasianthaea* includes perhaps 20 species ranging from Mexico to Panama and has been recorded from northern South America. Mr. Kenneth Becker of the New York Botanical Garden is now studying the group.

Literature:

Becker, K. M. 1972. Proposal to conserve the generic name 9216. *Zexmenia* A. Gray (1852) non LaLlave & Lexarza (1824) (Asteraceae). Taxon 21: 712–715.

Blake, S. F. 1917. New and noteworthy Compositae. Contr. Gray Herb. 52: 1–106.

———. 1930. Notes on certain type specimens of American Asteraceae in European herbaria. Contr. U.S. Natl. Herb. 26: 227–263.

Jones, W. W. 1905. A revision of the genus *Zexmenia*. Proc. Amer. Acad. Arts 41: 143–167.

a. Plants more than 50 cm tall; leaves mostly more than 10 mm wide; involucral bracts more than 5 mm wide ---------- 1. *L. fruticosa*

aa. Plants less than 30 cm tall; leaves mostly less than 10 mm wide; involucral bracts less than 3 mm wide ---------- 2. *L. nowickeana*

1. **Lasianthaea fruticosa** (L.) K. M. Becker, Phytologia 31: 297. 1975.—Fig. 62.

Bidens fruticosa L., Sp. Pl. 833. 1753. Based on Bidens foliis ovatis serratis petiolatis, caule fruticosa L., Hort. Cliff. 399. TYPE: Central America, Hort. Cliff. (BM, not seen, GH, photo).

Verbesina fruticosa L., Sp. Pl., ed. 2. 1271. 1763. Based on Bidens foliis ovatis serratis petiolatis, caule fruticosa L., Hort. Cliff. 399. TYPE: Central America, Hort. Cliff. (BM, not seen).

Bidens frutescens Miller, Gard. Dict., ed. 8. 1768. TYPE: Carthasuna, (BM, not seen).

Zexmenia costaricensis Benth. in Örsted, Vidensk. Meddel. Dansk Naturhist. Foren. Kjøbenhavn 1852: 95. 1852. TYPE: Costa Rica, *Oersted* (not seen).

Z. nicaraguensis C. Muell. in Walp., Ann. Bot. Syst. 5: 226. 1858, sphalm.

Narvalina fruticosa (L.) Urb., Symb. Antil. 5: 265. 1907.

Zexmenia frutescens (Miller) Blake, Contr. Gray Herb. 52: 50. 1917, not Z. *fruticosa* Rose, Contr. U.S. Natl. Herb. 1: 103. 1891.

Z. frutescens var. *genuina* Blake, Contr. Gray Herb. 52: 51. 1917. Based on Z. *frutescens* (Miller) Blake var. *frutescens*.

Shrub or *tree* to 5 m tall; branches slender, striate, gray or brown, twigs puberulent with appressed, ascending hairs, glabrescent. *Leaves* opposite, simple, ovate, apically acuminate, basally obtuse, to ca. 14 cm long, the margins serrate,

the veins ascending-pinnate, above appearing 3-nerved from near the base, elevated and fine reticulate beneath, scabrous above with scattered, white-based verrucose hairs, softly pubescent beneath with sturdy hairs on the veins, glabrate on the lamina; petiole 6–9 mm long, slender, pubescent above, an intrapetiolar ridge present and prominent after leaf fall. *Inflorescences* with several heads, compound, subumbellate, cymose or round-topped panicles; pedicels puberulent, 2–3 cm long, linear bracts sometimes present. *Heads* radiate, ca. 3 mm across; involucre 8–10 mm tall, cylindrical to campanulate, the 4 outermost bracts basally imbricate, equalling or overtopping the disc florets, oblong, apically darker and deltoid, indurate, evenly puberulent and ciliate, the innermost bracts shorter, less pubescent; receptacle nearly flat; paleas scarious, enfolding the floret, apically acute-cuspidate, ciliate on the costa and margins, otherwise glabrous, about as long as the awns, much shorter than the corolla; ray florets few, the ligule showy yellow, ca. 20 mm long, spathulate, 1-notched, the style branches flattened, glabrous, the ovary fertile, sharply trigonous, 3-awned; disc florets numerous, ca. 8 mm long, the corolla tubular, ca. 6 mm long, the tube ca. 2 mm long, the throat cylindrical, glabrous, the 5 lobes ventrally pubescent, the anthers ca. 3 mm long, dark, the appendages lighter, the auricles obscured by a truncate apical expansion of the filaments, the style branches lanceolate, dorsally pilose, the base not expanded, immersed in the 1 mm tall, apically erose, cylindrical nectary, the ovary fertile, flat, glabrous, thin-winged, the pappus of two stout awns and united by a squamellous ring. *Achene* black, shiny ca. 5 mm long, strongly 2–3-angled, flat, the margins yellow; pappus of awns inserted near the edges of the achene apex, mostly shorter than the achenes, stout, ascending-strigulose, the dorsal angles continued by thin, scarious tissue to the sides of the achene, the awns united by a short or long, fimbriate ring of scales.

CHIRIQUÍ: Near San Félix, eastern Chiriquí, *Pittier 5455* (GH, NY). COCLÉ: Near El Valle, 800–1000 m, *Allen 749* (GH, MO). Penonomé, *Dwyer 2015* (MO). Between Las Margaritas and El Valle, *Woodson et al. 1748* (GH, MO, NY). PANAMÁ: Road to Cerro Campana, ¼ mi from Pan-Am. Hwy., *Croat 12032, 12039* (both MO). Near top of Cerro Campana, *Duke 6018* (GH, MO). Cerro Campana, 2400–2700 ft, *Duke 8692* (MO). Cerro Campana, *Ebinger 372* (MO, NY); *McDaniel 6922a* (MO). Road to Cerro Campana, *Tyson 6421* (MO). VERAGUAS: Hills W of Soná, 500 m, *Allen 1038* (MO).

2. **Lasianthaea nowickeana** D'Arcy, Phytologia 30: 6. 1975. TYPE: Panama, *Duke et al. 3632* (MO).—FIG. 63.

Weak, sprawling *herb* to 30 cm long, branching at the base, rooting at the lower nodes; stem slender with ascending verrucose hairs, glabrescent, the surface becoming chartaceous, tan colored. *Leaves* mostly 3–4 cm long and 5–9 mm wide, oblanceolate, apically obtuse or acute, mucronulate, basally acute, the margins callose-serrate, veins ca. 4 on each side of the midvein, anastomosing near the margins and not running directly to the teeth, fine-reticulate and ascending-pubescent beneath with appressed white, verrucose hairs, a few scattered hairs above, drying much lighter beneath; petioles short, canaliculate above. *Inflorescence* a solitary terminal head but sometimes 2–3 aggregated on a stem; peduncle ascending-pubescent, ebracteate. *Heads* inconspicuously radiate, obconical; involucral bracts lanceolate, imbricate, about 7, the outermost ca. 7 mm long,

Figure 62. *Lasianthaea fruticosa* (L.) K. M. Becker. Habit (× 7/10). [After *Woodson et al. 1748* (MO).]

lanceolate, stiff, with ascending, stiff hairs, the apical half distinctly darker green, the innermost narrower, slightly longer, the margins serrulate, the apical half not so clearly marked, glabrate; paleas like the inner involucral bracts but narrower, glabrous, the margins serrulate, only partly enfolding the florets; ray florets several in one series, 10–16 mm long, the corolla yellow, the ligule 2 mm wide, 3–4 mm long, deeply 2-lobed, glabrous, 6-nerved, the tube elongate, ca. 7 mm long, pubescent, especially apically, the style branches slender, long exserted, the ovary fertile, linear, 3-angled, the angles ascending-strigose with brownish glandular spots, pappus of 4 stout, erect, strigulose awns with distinct, swollen bases, the carpopodium inconspicuous; disc florets numerous, 9–10 mm long, the corolla yellowish, narrowly tubular, expanding gradually upwards, pilose just above the middle with a few scattered hairs above and below, the 5 small yellow lobes porrect, ventrally pilose, the anthers black, ca. 2 mm long, the appendages yellowish, basally obtuse, the anther column 0–3 mm long, orange, the filaments glabrous, white, the style branches lanceolate, pubescent, the style base not expanded, the ovary linear, 3-angled, the angles ascending-strigose, apically 2–3-awned, the awns unequal, 7–8 mm long, pappus mostly of 2 awns and a ring of small scales. *Achene* not seen.

This species is distinctive in its straight, acute, smooth involucral bracts and small oblong oblanceolate leaves. The elongate tube and broad ligule of the ray florets are distinctive as well. It is known only from one collection.

SAN BLAS: Along river, headwaters of Río Cuasí, *Duke et al.* 3632 (MO).

62. MELANTHERA

Melanthera Rohr, Skr. Naturhist.-Selsk. 2: 213. 1792. TYPE: *Bidens nivea* L. = *Melanthera nivea* (L.) Small.

Amellus P. Browne, Civ. Nat. Hist. Jam. 317. 1756, nom. rejic., not *Amellus* L., Syst. Nat., ed. 10: 1225, 1377. 1759, nom. cons. Published without species.

Melanthera Michx., Fl. Bor. Amer. 2: 106. 1803. TYPE: *M. hastata* Michx. = *M. nivea* (L.) Small.

Lipotriche R. Brown, Trans. Linn. Soc. London 12: 118. 1817, not Less., Syn. Gen. Comp. 231. 1832. Published without species. LECTOTYPE: *L. brownei* DC. = *Melanthera scandens* (Schum. & Thonn.) Roberty.

Psathurochaeta DC., Prodr. 5: 609. 1836. TYPE: *P. dregei* DC. = *Melanthera scandens* subsp. *dregei* (DC.) Wild.

Wuerschmittia Schultz-Bip., Flora 24, Intell. 27. 1841, nom. nud. TYPE: *W. abyssinica* Schultz-Bip. ex A. Rich. = *Melanthera* (A. Rich.) Benth. & Hook.f.

Echinocephalum Gardn., Hooker's Jour. Bot. Kew Gard. Misc. 7: 294. 1848. LECTOTYPE: *E. latifolia* Gardn. = *Melanthera latifolia* (Gardn.) Cabr.

Herbs or *vines*, mostly perennial; stems drying sulcate, pubescent with appressed, ascending, stout-based verrucose hairs, often glabrescent, the nodes with an interpetiolar ridge. *Leaves* opposite, often decussate, sometimes verticillate, lobed or not, the margins mostly crenate or dentate, mostly 3-nerved from the base, often scabrous, especially above, membranaceous; sessile or petiolate. *Inflorescence* undifferentiated, the few heads paniclelike, open; pedicels slender, elongate. *Heads* globose, discoid (Panama) or radiate; involucral bracts in several somewhat unequal imbricate series, ovate to lanceolate, acute or obtuse, indurate,

FIGURE 63. *Lasianthaea nowickeana* D'Arcy. Habit (× ⅜). [After *Duke* 3632 (MO).]

apically green, basally stramineous, mostly puberulent with whitish hairs which obscure the venation; receptacle convex; paleas indurate, thickening upwards, apically obtuse or cuspidate, dorsally puberulent, half-enfolding the florets; ray florets (when present) few in one series with conspicuous, white, yellow or orange ligules, the style present or not, the ovary sterile; disc florets numerous, the corolla tubular, the 5 lobes dorsally pubescent, the stamens 5, the anthers with expanded, cordate, infolded appendages, the adjacent basal auricles connate, the style branches flattened, acuminate, the base not expanded, the ovary slender, 3–4-sided, broadening upwards, the nectary cylindrical, apically entire or minutely irregular, expanded basally, the pappus caducous, of 2–several weak awns and few or numerous hairs, often in more than 1 series. *Achenes* plump, somewhat compressed, 3–4-angled, apically truncate, the pericarp thin, whitish or yellowish, the endocarp black, stony; carpopodium evident; pappus mostly wanting.

Melanthera comprises 20–25 species of the tropics and subtropics of both the New and Old Worlds. Those in the New World north of Colombia are perennial herbs with white, rayless flowers. Two of these species, *M. nivea* (L.) Small and *M. aspera* are widespread and differ mainly in the apices of the palea (Fig. 64). Parks (1968) recognized several unusual groups of Florida as distinct species and a seaside race of *M. aspera* in Panama and other parts of the Caribbean area as a distinct variety. In Panama, only *M. aspera* is present and the seaside variety cannot be distinguished. Some collections from the savannas near Panama City match collections from Florida and other localities which Parks referred to *M. angustifolia*. These are considered to be ecotypes adapted to situations of impeded drainage and are recognized as *M. aspera* var. *subhastata*, but they might better be treated at a lower rank.

In Africa and southeastern South America, *Melanthera biflora* (L.) Wild and *M. latifolia* (Gardn.) Cabr. are herbs with small rays. The two species occur on different continents and are separated by differences in the length of the palea tips, differences of the same sort as those which separate *M. nivea* and *M. aspera* in the Caribbean region. Most other species are large, scandent plants of forests with showy yellow radiate heads. These forest species, which occur in both Africa and ultramontane South America, approach *Wulffia* in most features, and the fruits, although baccate in *Wulffia* and stony in *Melanthera*, are of the same general appearance. Evolution would appear to have gone from scandent, large showy forest plants to herbaceous habit and then to loss of rays and a shift to white flowers. These advanced members of the genus are the ones found in our area.

Melanthera is also closely related to *Pascalia glauca* Ort. of South America, which has narrow leaves and involucral bracts. It is more closely related to the species of *Melanthera* than to those of *Wedelia* where it has usually been placed.

Melanthera was published without species, and the type species was designated by Cassini (Dict. Sci. 29: 488. 1823.). Strother's (Taxon 19: 336. 1970.) designation of *M. panduriformis* Cass. as lectotype cannot be accepted.

In Panama, species of *Melanthera* are mostly ruderal weeds, best recognized by the membranaceous, scabrous, opposite leaves and by the globose heads of

whitish florets. They are of no known use and have no known common name in Panama.

Both Seemann (Bot. Voy. Herald 156. 1854.) and Hemsley (Biol. Cent. Amer. Bot. 2. 163. 1881) reported *Melanthera hastata* Michx. from Panama. Parks (1968, 1973) placed this name in synonymy under *M. nivea*. This species occurs around the Gulf of Mexico but is not otherwise known from regions near Panama. It differs from *M. aspera* in the length of its paleas and in other small details, and confusion of the two species is facile. Hemsley cited *Fendler 165* from Panama but this collection was not seen in this study nor was it cited by Parks. The Seemann and Hemsley reports may be based on misidentification.

Literature:

Parks, J. C. 1968. A revision of the genus *Melanthera* Rohr. (Compositae) in North America and the Caribbean. Ph.D. thesis, Vanderbilt University.

———. 1973. A revision of North American and Caribbean *Melanthera* (Compositae). Rhodora 75: 169–210.

Wild, H. 1965. The African species of the genus *Melanthera* Rohr. Kirkia 5: 1–5.

a. Leaves less than 4 cm long and 1.5 cm wide; plants of impeded drainage, savannas, etc. ———— 1b. *M. aspera* var. *subhastata*

aa. Leaves more than 4 cm long and 1.5 cm wide; plants of many habitats ———— 1a. *M. aspera* var. *aspera*

1. **Melanthera aspera** (Jacq.) Small, Bull. Torrey Bot. Club 36: 164. 1909.— FIG. 64.

1a. **Melanthera aspera**[42] var. **aspera**.

Calea aspera Jacq., Coll. 2: 290. 1788 (1789); Ic. Pl. Rar. 3: 15, *tab.* 583. 1789. TYPE: not seen.

Melananthera deltoidea Michx., Fl. Bor. Amer. 107. 1803. Based on *Calea aspera*.

Melanthera urticaefolia Cass., Dict. Sci. Nat. 29: 484. 1823. Based on *Melananthera deltoidea* Michx. and *Calea aspera* Jacq.

Amellus asper Kuntze, Rev. Gen. Pl. 1: 305. 1891. Based on *Calea aspera* Jacq.

A. asper var. *glabriusculus* Kuntze, Rev. Gen. Pl. 1: 305. 1891. TYPE: Panamá, Colón, ?*Kuntze* (NY, not seen).

Melanthera brevifolia O. E. Schulz in Urb., Symb. Antil. 7: 123. 1911. TYPE: Cuba, *Ekman 15505* (NY).

M. hastata var. *cubensis* O. E. Schulz in Urb., Symb. Antil. 7: 123. 1911. TYPE: Cuba, *Wright 3600* (NY).

M. crenata O. E. Schulz in Urb., Symb. Antil. 7: 123. 1911. TYPE: Bahamas, New Providence, *Northrop & Northrop 58* (NY).

M. calcicola Britt. in Britt. & Wils., Sci. Surv. Puerto Rico 6: 309. 1925. TYPE: *Britton et al. 6784* (NY).

M. confusa Britt. in Britt. & Wils., Sci. Surv. Puerto Rico 6: 309. 1925. TYPE: Tortola, *Fishlock 440* (NY).

M. aspera (Jacq.) Rendle in Fawcett & Rendle, Fl. Jamaica 7: 232. 1936, redundant comb.

M. aspera (P. Brown) D'Arcy, Phytologia 30: 6. 1975, superfluous comb.

Erect or sprawling perennial *herb* to 80 (150) cm; stems drying sulcate, sparingly appressed-pubescent with verrucose hairs, lower nodes with a con-

[42] A number of other synonyms were cited by Parks (1968), but only the names listed relate to Panamanian material.

spicuous interpetiolar ridge. *Leaves* opposite, ovate, 5–11 cm long, apically acuminate, basally obtuse, truncate or hastate-lobed, marginally serrate, 3-veined from the base, drying darker above, scabrous, the many-celled bases of the short hairs sometimes imparting a punctate appearance, drying green beneath, sparingly pubescent with reduced, more or less appressed simple hairs and with tufts in the axils of the secondary veins; petiole slender, 1–3 cm long. *Inflorescence* undifferentiated, 1–several terminal or subterminal heads on slender, sulcate, ascending, 0.5–5 cm long pedicels; one or more minute linear bracts sometimes present at or near the base. *Heads* discoid, globose, 8–12 mm across; involucral bracts in 2–3 imbricate, somewhat unequal, similar series, ovate, acute, indurate, apically green, basally ochraceous or stramineous, the venation obscured by numerous, appressed, ascending whitish hairs, 2–3 mm long; receptacle convex, white, 3–4 mm across; paleas indurate, thickening upward, apically obtuse with a short (less than 1 mm long) cusp, many nerved, enfolding the florets, the keel slightly excurrent; florets ca. 7 mm long, the corolla tubular, ca. 5 mm long, the 5 white lobes acute, long-papillose on the dorsal surface and on the margins, the tube short, not basally expanded, outside with minute ascending hairs, the stamens ca. 5 mm long, the appendages deltoid, infolded, the adjacent auricles connate, the style branches long acuminate, the style base not expanded, the ovary 3–4-angled, the nectary columnar, 0.5 mm tall, expanded in the basal half, the pappus caducous, of 2–several weak bristles and a ring of short hairs or scales, often in more than 1 series. *Achene* ca. 2 mm long, 3–4-angled slightly compressed, broadening upward, greyish or brownish, the pericarp thin, whitish or yellowish, the endocarp black, striate, stony; carpopodium yellow, the apex truncate, sometimes recessed; pappus mostly wanting.

Melanthera aspera is a frequent weed of roadsides, fields, and shores of lowland Panama. It is recognizable by its whitish globose heads and plump apically truncate achenes. This species ranges from Florida to Panama and Venezuela. Plants of seacoasts may have fewer, more appressed trichomes and slightly longer palea apices and were recognized by Parks (1968) as var. *glabriuscula*. This distinction is not evident in Panamanian plants.

BOCAS DEL TORO: Santa Catalina, *Blackwell et al. 2714* (MO). Almirante, *Blum 1319* (MO). Bocas del Toro, *Carleton 154* (US). Changuinola Valley, *Dunlap 336* (GH). Chiriquicito to 5 mi S along Río Guarumo, *Lewis et al. 2088* (MO). Lower Changuinola, *Stork 135* (MO). Without definite locality, *Wedel 271* (GH, MO). Isla Colón, *Wedel 538* (MO). Water Valley, *Wedel 751* (MO), *931* (MO, US). Near Chiriquí Lagoon, *Wedel 1339* (MO), *1797* (MO, US). Old Bank Island, *Wedel 1962* (MO). Changuinola River, *Wedel 2602* (MO, US). Near Nievecita, *Woodson et al. 1818* (MO, NY, US). CANAL ZONE: Matachin, *Cowell 191* (NY). Colón to Empire, *Crawford 402* (NY). 2½ mi N of Gamboa gate, *Croat 9343* (MO, NY). Railroad near Pedro Miguel, *Croat 7148* (MO). Hill S of Pedro Miguel locks, *Croat 9177* (MO). 1 mi N of Summit Garden, *Croat 12866* (MO). Road C21 3 mi from Gaillard Hwy., *Croat 13003* (MO). Fort Sherman, *Duke 4335* (MO). Madden Dam, *Dwyer 3040* (NY). Chagres, *Fendler 164* (NY). Outskirts of Ancón, *Greenman & Greenman 5045* (GH, MO). Between Gamboa and Darién, *Heriberto 33* (US). Chagres River, ca. 3 mi above Gamboa Bridge, *Kennedy et al. 2289* (MO). Between Frijoles and Monte Lirio, *Killip 12115* (GH, US). Fort Sherman, *Lazor & Blum 5388* (MO). Between Rodman Marine Base and Chorrera, *Nowicke et al. 3607* (MO). Corozal, *Piper 5296* (GH, US). Empire to Mandinga, *Piper 5570* (GH, US). Río Grande near Culebra, *Pittier 2101* (NY, US). Balboa, *Standley 25556, 32135* (both GH, US). Near Summit, *Standley 25778* (US). Corozal road near Panamá,

A
B

Standley 26790 (US). Near Gatún, *Standley 27220* (US). Frijoles, *Standley 27650* (US). Near Fort Randolph, *Standley 28749* (US). Between Fort Clayton & Corozal, *Standley 29008* (US). Obispo, *Standley 31211* (US). Summit, *Standley 26920* (US). Fort Sherman, *Tyson 2263* (MO). Curundu, *Tyson & Blum 2527* (MO). 6 mi N of Gamboa, *Tyson 3499* (MO). Fort San Lorenzo, *Tyson & Blum 3672* (MO). BARRO COLORADO ISLAND: *Croat 12945* (MO); *Shattuck 537* (MO); *Wetmore & Abbe 37* (GH, MO); *Woodworth & Vestal 395* (GH, MO). CHIRIQUÍ: San Bartolo Limite, *Busey 538* (MO). Bajo Mono, Boquete District, *Davidson 499* (GH, MO). From Boquete to 3 mi N, *Lewis et al. 636* (MO, US). Near Boquete, *Maurice 701* (US). Near San Félix, *Pittier 5153* (GH). Río Caldera beyond Bajo Mono, 1700 m, *Wilbur et al. 11054* (MO). COCLÉ: Near El Valle de Antón, *Croat 13279* (MO). Ridge S of El Valle, *Gentry 6802* (MO). El Valle de Antón, *Lewis et al. 2524* (MO). Boca del Toabre at Río Cocle del Norte, *Lewis et al. 5504* (MO). Cerro Pilón above El Valle de Antón, 2000 ft, *Porter et al. 4641* (MO). Bismark above Penonomé, *Williams 281* (NY, US). COLÓN: Miguel de la Borda, *Croat 10049* (MO). Near Portobelo, *D'Arcy & D'Arcy 6689* (MO). María Chiquita E of Río Piedras, *Dwyer & Kirkbride 7791* (MO, NY). Portobelo, *Ebinger 128, 448* (both MO). Near Salamanca, *Gentry 6715* (MO). Manzanillo Island, *Hayes 4* (US), *687* (NY). Aspinwall, *Hayes 845* (NY). Mouth of Río Piedras, *Lewis et al. 3183* (MO). Porvenir, *Montgomery 207* (MO). Without definite locality, *Tyson et al. 4528* (MO). DARIÉN: Río Balsa, *Duke 8721* (MO). Río Piñas, *Duke 10553* (MO). Around Puerto Obaldía, *Pittier 4403* (US). LOS SANTOS: 5 mi S of Pocrí, *Croat 9734* (MO). Punta Mala, *Tyson 2721* (MO). PANAMÁ: Taboga Island, *Allen 138* (MO). Las Sabanas, *Celestine 113* (US). Cerro Azul, *Dwyer 2179* (MO). San José Island, *Johnston 1103, 1203* (both US). Taboga Island, *Killip 3203* (NY), *3206* (US). Chimán, *Lewis et al. 3288* (MO). Las Sabanas, *Macbride 2643* (US); *Paul 191* (US). Matías Hernándes, *Pittier 2899* (US). Old Panama, *Porterfield 1933* (NY). Río Tapia, *Standley 28064* (US). Cerro Azul, *Tyson 6322* (MO). SAN BLAS: Near Puerto Obaldía, *Croat 16869* (MO). Airport at Irandí, *Duke 6516* (GH, MO). Puerto Obaldía, *Gentry 1572* (MO). Soskatupu, *Kirkbride 204* (MO, NY). VERAGUAS: 5 mi W of Santa Fe, *Croat 23036* (MO).

1b. **Melanthera aspera** var. **subhastata** (O. E. Schulz) D'Arcy, comb. nov.

M. angustifolia A. Rich. in Sagra, Hist. Cuba 11: 54. 1850. TYPE: Cuba, Isle of Pines, *Sagra* (P).

M. microphylla Steetz, Bot. Voy. Herald 1561. 1854. TYPE: Panamá, *Seemann 254* (BM, photo MO).

M. linearis Blake, Contr. U.S. Natl. Herb. 24: 30. 1922. TYPE: Guatemala *Blake 9601* (GH).

M. angustifolia var. *subhastata* O. E. Schulz, Repert. Spec. Nov. Regni Veg. 26: 109. 1929. TYPE: Cuba, *Ekman 12359* (NY).

M. amellus var. *subhastata* (O. E. Schulz) D'Arcy, Phytologia 30: 6. 1975.

Slender, erect or sprawling *herb* to 70 cm tall, glabrate. *Leaves* opposite, lanceolate to oblong, sometimes basally short-lobed, apically obtuse or acute, basally narrowed or obtuse, the margins crenate-serrate, 1-nerved, both sides puberulent with weak, short hairs and scabrous on the veins with longer, ascending, stout-based hairs; petioles short or wanting. *Inflorescence* not differentiated; peduncles to 5–6 cm long, slender, arising terminally or subterminally. *Heads* discoid, globose, whitish, to 12 mm across; involucral bracts in ca. 3 similar, somewhat unequal series, ovate, obtuse, indurate, apically green, basally stramineous or ochraceous, the venation obscured by numerous, fine, whitish, ascending hairs; receptacle convex; paleas indurate, conspicuously many-nerved, obtuse with an apical cusp 0.5–1 mm long; ray florets wanting; disc florets presumably resembling those in the typical variety. *Achene* not examined.

Melanthera aspera var. *subhastata* has been recognized as a distinct species

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FIGURE 64. *Melanthera aspera* (Jacq.) Small.—A. Habit (× ⅗). [After *Gentry 2263* (MO).]—B. Floret (× 7½). [After *Tyson 2263* (MO).]

by several workers, but it seems to represent an edaphic response of populations of *M. aspera* to habitats with impeded drainage. It has small leaves, weaker stems, less pubescence, and blunter involucral bracts than the typical variety. Reports of var. *subhastata* are known (Parks, 1968) from a number of widespread localities within the range of typical *Melanthera aspera*, e.g., Panama, Guatemala, Mexico, Florida, and the Greater Antilles.

PANAMÁ: Near Río Pacora E of Panama City, *Bartlett & Lasser 16466* (MO). Near Las Sabanas, *Standley 4077* (US). Las Sabanas, ?*Zetek 1932* (MO). Río Tataré, *Woodson & Schery 1004* (MO).

63. MONTANOA

Montanoa Cerv. in LaLlave & Lexarza, Nov. Veg. Desc. 2: 11. 1825. TYPE: *M. tomentosa* Cerv.

Montagnaea DC., Prodr. 5: 564. 1836. Based on *Montanoa* Cerv.

Shrubs or *trees*; branches slender. *Leaves* opposite, entire or lobed, sometimes toothed or crenate, 3-nerved from above the base; petioles mostly slender, sometimes partly winged, mostly pubescent and glandular. *Inflorescences* mostly open panicles; peduncles slender; bracts and bracteoles foliaceous to scalelike. *Heads* radiate, sometimes showy; involucral bracts in two dissimilar series, the outermost 5–8, narrow, herbaceous, sometimes unequal, the innermost smaller, often inconspicuous, apiculate or spinose; paleas enfolding the florets, apiculate, accrescent and persistent in fruit, becoming chartaceous to coriaceous, sometimes spine-tipped; ray florets with an elongate, spathulate ligule, sometimes glandular, the tube short, the ovary sterile; disc florets numerous, the corolla limb tubiform, 5-lobed, the tube mostly short, the anthers with deltoid appendages, the style branches slender, clavate, truncate, sometimes apiculate, the ovary fertile or those of the central florets abortive. *Achenes* obovate, laterally compressed; pappus wanting.

Montanoa includes numerous species in Mexico and Guatemala and a few others in Central and South America. Only one species is known from Panama. The accrescent apiculate paleas which loosely envelop the achenes readily identify fruiting collections.

1. **Montanoa hibiscifolia** (Benth.) Standley, Contr. U.S. Natl. Herb. 23: 1533. 1926.—FIG. 65.

Montagnaea hibiscifolia Benth. in Örst., Vidensk. Meddel. Dansk Naturhist. Foren. Kjøbenhavn 1852: 89. 1852. TYPE: not seen.
Montanoa hibiscifolia (Benth.) D'Arcy, Phytologia 30: 5. 1975, redundant comb.

Shrub to 4 m tall; branches slender, puberulent with a mixture of erect, spreading, long-celled hairs and weak, collapsed, reddish, short-celled hairs. *Leaves* opposite, to 25 cm long, mostly 3–9-lobed, deltoid to broadly ovate, apically acuminate, basally obtuse, truncate or cordate, the sinuses rounded, the margins irregularly crenate-dentate, 3-veined from near the base, softly tomentose and glandular beneath, tomentulose and drying darker above; petiole to 15 cm long, tomentose and canaliculate on the dorsal surface, basally expanding to clasp

FIGURE 65. *Montanoa hibiscifolia* (Benth.) Standley. Fruiting branch (× ⅔). [After *White & White 113* (MO).]

the stem, sometimes apically auriculate. *Inflorescence* an open, many flowered panicle; rachis and pedicels tomentulose; paired bracts decreasing in size upwards; bracteoles scalelike, sometimes solitary along the ultimate branches. *Heads* radiate, showy, 2.5–3 cm across in flower, 2–2.5 cm across in fruit; involucral bracts lanceolate, ca. 3 mm long, herbaceous, grey-puberulent, spine-tipped; paleas completely enfolding the ovary and only slightly exceeding it; ray florets 6–10 in one series, the corollas with a short tube and the limb 10–15 mm long, narrowly spathulate, denticulate, dorsally puberulent and glandular, ovary abortive; disc florets numerous forming a globose disc 7–8 mm across, the limb broadly tubular, the lobes incurved, the tube short, ascending pubescent and glandular, the anthers ca. 1.8 mm long with hyaline apical lobes, basally obtuse or subauriculate, the style branches cuneiform, the style base slightly contracted, the nectary a large, cupular, stipitate structure, the ovary quadrangular, pappus a single short, stout, deciduous awn. *Achene* dark, quadrate, rugulose, glabrous, epappose, ca. 3 mm long.

Montanoa hibiscifolia is a large, apparently open shrub with slender branches and large, lobed leaves. The heads enlarge and change dramatically in appearance as the slender, porrect, yellow or white ligules disappear and the paleas enlarge into papery, minutely striate sacs loosely enveloping the small achenes. In some species of *Montanoa*, the paleas develop conspicuous, recurved apical hooks, but in this species the apices become small, straight bristles.

Montanoa has been collected only once in Panama. It ranges to Mexico (Chiapas). The type locality is in Costa Rica.

CHIRIQUÍ: Valley of the upper Río Chiriquí Viejo, *White & White 113* (MO).

64. OYEDAEA

Oyedaea DC., Prodr. 5: 576. 1836. TYPE: *O. verbesinoides* DC.

Large, erect, branched *herbs*; stems villous. *Leaves* opposite, simple, ovate, elliptical or obovate, often narrow, the margins crenate-serrate, 3-veined from well above the base, tomentose; petioles mostly distinct, articulating at the base and leaving conspicuous ridges on the stem. *Inflorescence* an open, several–many-flowered panicle; bracts foliaceous; bracteoles sometimes present, opposed or not. *Heads* radiate, showy; involucral bracts numerous in several graded series, loosely imbricate, lanceolate, apically acute, indurate and even in texture, the veins obscure, puberulent; paleas scarious, conduplicate around the floret, with a ligulate apical appendage; receptacle slightly convex; ray florets several in 1 series, the corolla yellow, the ligule conspicuous, emarginate, pubescent on the veins, the androecium and style wanting, the ovary sterile, trigonous, the pappus with 3–4 awns and a row of short hairs; disc florets numerous, the corolla tubular, slightly expanded into a cylindrical limb, the 5 lobes dorsally puberulent, the anthers and narrowly deltoid appendages black, the basal auricles inconspicuous, the style branches with a short, pubescent apicule, the style basally immersed in a cylindrical, 1 mm tall, apically erose nectary, the ovary laterally flattened,

pilose. *Achene* compressed with a suggestion of wings, glabrate; pappus a dense ring of basally concrescent hairs and two strigose awns.

Oyedaea includes a few species of South America and one species ranges through Central America into Mexico. It is distinguished mainly by its pappus which consists of two awns plus an intermediate ring of scalelike, basally fused hairs. The awns (Fig. 66) are not inserted at the edges of the achene as in *Lasianthaea*, but closer to the center. They at first move outwards and then bend back to point upwards. The loosely imbricate, narrow involucral bracts are also distinctive.

1. **Oyedaea verbesinoides** DC., Prodr. 5: 577. 1836. TYPE: Venezuela, *Vargas 191* (G-DC, not seen, IDC. DC. Prod. 946. II. 5).—FIG. 66.

Large *herbs* to 5 m tall; stems villous-tomentose, faintly ridged. *Leaves* opposite, ovate, to 15 cm long, apically acuminate or acute, basally acuminate, acute or obtuse, the margins crenate-serrate, 3-veined from well above the base, above scabridulous with ascending, stout based hairs, softly tomentose beneath; petioles thin-winged and appearing canaliculate, articulating at the base and leaving conspicuous annular ridges on the stem. *Inflorescence* paniculate, somewhat rounded or flat-topped, several–many-headed; peduncles bracteolate. *Heads* showy, yellow, radiate, to 6 cm across; involucral bracts numerous in several graded series, loosely imbricate, lanceolate, the innermost ca. 10 mm long, apically acute and callose-mucronulate, the veins obscure, indurate but remaining evenly green, puberulent with appressed or ascending hairs; paleas scarious, conduplicate around the floret, the apex with a ligulate appendage, 10–11 mm long; receptacle slightly convex; ray florets several in 1 series, the corollas yellow, 15–20 mm long, broad, emarginate, the veins pubescent, the style wanting, the ovary trigonous, pappus with 3–4 awns and a row of short hairs; disc florets numerous, the corolla tubular, ca. 15 mm long, the tube glabrous, ca. 3 mm long, slightly expanded into a cylindrical limb, the 5 lobes dorsally puberulent, the anthers and appendages black, narrowly deltoid, 4 mm long, basally auriculate but the filaments darkened and thickened to give a truncate appearance, the style apically puberulent, the branches with a short, pubescent apicule, the base immersed in a cylindrical, 1 mm tall, apically erose nectary, the ovary laterally flattened, pilose with long ascending hairs. *Achene* black, ca. 5 mm long, compressed with a suggestion of wings, glabrate; pappus a dense thick ring of basally concrescent hairs and two strigose, easily detached awns.

Oyedaea verbesinoides is superficially similar to *Tithonia* in its large size and showy radiate yellow flowers, but differs in its tomentose stems, relatively slender peduncles and involucral bracts, and in its pappus which lacks large scales. The species occurs at lower to upper elevations in western Panama. It blooms mainly from November to February but collections have been taken in other months.

CHIRIQUÍ: Boquete, 3800 ft, *Davidson 827* (GH, MO, US). Near Volcán, 4600 ft, *Duke 9183* (MO, US). Boquete, *Dwyer 6970* (MO). Near Boquete, 3300–4200 ft, *Lewis et al. 631* (GH, MO, US). Sierra del Boquete, 1380 m, *Maurice 724* (MO, US). Around Boquete, *Pittier 2948* (US). Camiseta, Volcán de Chiriquí, 7500 ft, *Terry 1339* (GH, MO). COCLÉ:

FIGURE 66. *Oyedaea verbesinoides* DC.—A. Habit (× 7/10).—B. Achene (× 6⅗). [After *Lewis et al. 3106* (MO).]

Near El Valle, 800–1000 m, *Allen 79* (MO, US). S of El Valle de Antón, 600–800 m, *Allen 2866* (MO, US). La Mesa to El Valle, ca. 2500 ft, *Dwyer & Duke 8289* (MO). S of El Valle de Antón, 600 m, *Gentry 6797* (MO). El Cope, 1500 ft, *Tyson 6097* (MO). HERRERA: 10 mi S of Ocú, *Tyson et al. 2846* (MO). PANAMÁ: Above Campana, 600–800 m, *Allen 1306* (GH, MO,

NY, US). Road to Cerro Campana, *Croat 14675* (MO). SE slope of Cerro Campana, *Lewis et al. 3106* (MO). Road to Cerro Campana, 1500 ft, *Tyson 6422* (MO).

65. RUMFORDIA

Rumfordia DC., Prodr. 5: 549. 1836. TYPE: *R. floribunda* DC.

Large branching *herbs* or weak *shrubs* to 3 m tall; stems glabrescent, drying striate. *Leaves* opposite, simple, apically acuminate, basally acute, obtuse, rounded or hastate, often contracted into wings on the petiole, the margins serrate or crenate, sometimes with one or two prominent lobes or angles, the midvein dividing into 3 principal veins well above the base, the minor venation mostly pinnate, puberulent with weak, multicellular, uniseriate hairs; petioles mostly distinct, broadly winged apically or for the full length, the wings sometimes produced into basal auricles. *Inflorescences* mostly well differentiated open panicles; foliaceous bracts subtending the lowermost two or three branches; minute leaflike or scalelike bractlets present at the base of minor branches and pedicels. *Heads* radiate, sometimes showy; involucral bracts in two dissimilar series, the outer herbaceous, ca. 5, the innermost smaller, narrow, only slightly enfolding the outer achenes; ray florets numerous in one series, the ligules yellow, broad or narrow, entire or 1–3-notched, sometimes glandular or pubescent, the tube elongate, the ovary fertile; disc florets much more numerous than the rays, the corolla limb tubular, 5-lobed, basally expanded, pubescent or glandular, the tube slender, sometimes as long as the limb, the anthers light or dark, long-exserted, apically appendaged, basally subauriculate, the style branches slender, glabrate, the ovary fertile. *Achenes* obovoid, glabrous, slightly compressed; pappus wanting.

A genus of about a dozen species ranging from Mexico to Panama, *Rumfordia* is distinguished by its large outer involucral bracts and by the elongate tubes of the corollas. Only one species occurs in Panama.

Rumfordia is closely related to *Tetragonotheca* of the southern United States which differs in having more strongly angled achenes, relatively shorter corolla tubes, and the fixed number of 4 outer involucral bracts. Both *Tetragonotheca* and *Rumfordia* are closely related to *Polymnia*, differing mainly in having both ray and disc florets with fertile ovaries. The elongate corolla tubes of *Rumfordia* are unusual but such tubes are also found in *Sclerocarpus*. *Rumfordia* and *Sigesbeckia* lack verrucose hairs and it is likely that these genera are best placed in association with *Polymnia* and other Melampodiinae.

1. **Rumfordia polymnioides** Greenman, Proc. Amer. Acad. Arts 39: 99. 1903. TYPE: Costa Rica, *Tonduz 11947* (US).—FIG. 67.

Large branching *herb* to 3 m tall; stems pilose with white, weak, spreading, multicellular hairs, glabrescent, drying striate, fistulose. *Leaves* large, to 35 cm long, ovate, sometimes deltoid, apically acuminate or acute, basally truncate or acuminate, sometimes with 1–5 prominent, acuminate lobes, the margins minutely callose-denticulate, the sinuses little indented, 3 major veins departing well above the base, the secondary venation pinnate, more frequent on the lateral veins than

on the midvein, both sides puberulent with scattered weak hairs, glandular beneath; petiole elongate except on leaves near the inflorescence, prominently winged, basally auriculate. *Inflorescence* an open, many flowered, cymose panicle; rachis and pedicels spreading-pilose, slender; bracts resembling the leaves; bractlets scalelike, apically acute or rounded, ciliate. *Heads* radiate, but sometimes appearing disciform; outer involucral bracts ca. 5, porrect, ovate or elliptical, sometimes broad, to 15 mm long, herbaceous, 3-nerved, ciliate and dorsally pubescent, glabrate ventrally, the inner bracts narrow, much shorter, stramineous, dorsally pubescent; paleas acute, drying stramineous, pubescent, shorter than the disc; ray florets in one series, ca. 9 mm long, inconspicuous when dried, the corolla yellow, the limb broad, the tube as long as the limb, glandular-hispid, inserted obliquely with a basal enlargement, the ovary fertile, slightly compressed dorsiventrally; disc florets numerous, forming a flattened or convex disc 1–2 cm across, the corolla yellow, 6 mm long, the limb tubular, about as long as but many times the diameter of the tube, basally hispid, apically 5-lobed, the lobes with 1 or 2 dorsal hairs, the tube slender, basally pubescent, the base expanded into a glandular-hispid cone or pedicel, the anthers yellowish, ca. 1.3 mm long, with yellowish apical appendages, basally subauriculate, the style branches clavate, apically sparingly pubescent, the style base slightly expanded, the ovary plump, fertile. *Achenes* black, lachrymiform, with faint, sharp longitudinal striations, ca. 1.5 mm long; pappus wanting.

Rumfordia polymnioides is distinguished from other Panamanian Compositae by its patent, broad, herbaceous outer involucral bracts and by the hispid corolla tubes which are about as long as the limb. The plump, black seeds somewhat resemble those of *Polymnia*. Another species, *R. aragonensis* Greenman, was described from Costa Rica. It reportedly differs in its less pubescent involucral bracts. *Rumfordia polymnioides* is the earlier name.

This species is known in Panama only from the Chiriquí mountains.

CHIRIQUÍ: Near "New Switzerland," central valley of the Río Chiriquí Viejo, 1800–2000 m, *Allen 1413* (MO, NY, US). Entrance to canyon below Bambito, 5000 ft, *Tyson 7042* (PMA).

66. SALMEA

Salmea DC., Cat. Pl. Monsp. 57, 140. 1813, nom. cons. TYPE CONS.: *S. scandens* (L.) DC.

Salmia auct., not *Salmia* Cav. (Liliaceae), nom. rejic.
Hopkirkia Spreng., Novi Prov. Hort. Acad. Hal. 23. 1819. TYPE: *H. eupatoria* (DC.) Spreng. = *Salmea eupatoria* DC., nom. rejic.

Shrubs or *vines*; stems slender. *Leaves* opposite, ovate, entire or dentate, pubescent with simple hairs or glabrous; petiolate, the interpetiolar ridge sometimes conspicuous. *Inflorescences* congested, cymose panicles and axillary or terminal peduncles. *Heads* small, discoid, the involucral bracts broad, sometimes apiculate, in 1–3 unequal series; paleas indurate, enfolding the florets; florets small, deeply 5-lobed, the anthers appendaged, basally auriculate, the style branches rounded, dorsally papillose, the ovary compressed, ciliate on margins and apex. *Achene* black, ciliate; pappus of 1–3 unequal awns.

FIGURE 67. *Rumfordia polymnioides* Greenman—A. Inflorescence (× ½).—B. Central floret (× 4⅘). [After *Allen 1413* (NY).]

Salmea includes 3 or 4 species of tropical America. Only one species is known from Panama.

Literature:

Blake, S. F. 1915. A revision of *Salmea* and some allied genera. Jour. Bot. 53: 193–202.

1. **Salmea scandens**[43] (L.) DC., Cat. Pl. Monsp. 141. 1813.—FIG. 68.

Bidens scandens L., Sp. Pl. 833. 1753. TYPE: Mexico, Vera Cruz, Hort. Cliff. (BM, not seen).
Salmea grandiceps Cass., Dict. Sci. Nat. 47: 88. 1827. TYPE: not seen.

Scandent *shrub*, sometimes elongate; stems slender, glabrate, with long internodes. *Leaves* opposite, ovate, to 8 cm long, apically acute or acuminate, basally obtuse or rounded, the margins denticulate with minute, appendiform, distant teeth or entire, often drying yellowish-brown, 3-nerved from near the base, the midvein pinnately veined in the upper half, glabrate or pubescent with weak hairs, often barbellate in the vein axils beneath; petioles to 15 mm long, deeply canaliculate above. *Inflorescences* small panicles, the heads congested, subumbellate; peduncles minutely pubescent with short, erect or ascending, whitish hairs, with minute, foliaceous opposite bracts and the ultimate divisions with alternate scalelike bractlets. *Heads* small, 3–4 mm tall, 3–4 mm across, discoid; involucral bracts in several unequal series, broadly ovate and acuminate into a narrow, green, oblong and rounded apex, or ciliolate, dorsally puberulent; paleas indurate, dorsally puberulent, enfolding the ovary; florets exserted about halfway from the involucre, ca. 3 mm long, the corolla whitish, ca. 1.5 mm long, lobed about halfway down, the 5 lobes cuculate, dorsally puberulent, the anthers appendaged, the basal auricles fused, filaments glabrous, the style branches rounded, dorsally papillose, the style base contracted into the cylindrical nectary, the ovary compressed, ciliate, with ca. 3 weak or stout, unequal strigose awns. *Achenes* black, compressed, ciliate on the margins and apex with 1–3 short, unequal awns.

Salmea scandens ranges through tropical America, but is not common. It may be recognized by its scandent habit, congested inflorescences of discoid heads and by the paleas which envelop each floret. Superficially it may be mistaken for species of the Eupatorieae, e.g. *Mikania* or *Stevia* species, but these species lack paleas and their achenes lack awns. It is known in Panama from middle and lower elevations.

CANAL ZONE: Around Gamboa, *Pittier 3411* (US). Fort Clayton near old hospital building no. 519, *Tyson & Blum 3903* (MO). COCLÉ: Near Penonomé, *Williams 85* (NY, US). Bismark above Penonomé, 2000–3000 ft, *Williams 284* (NY).

67. SCLEROCARPUS

Sclerocarpus Jacq., Ic. Pl. Rar. 1: 17, *tab. 176.* 1781. TYPE: *S. africanus* Jacq. ex Murr.

Mostly erect, annual *herbs*, rarely perennial or *shrubs*; stems slender, pubescent. *Leaves* alternate, sometimes opposite below, ovate, elliptical or filiform-dissected, the margins mostly serrate, 3-veined from near the base, pubescent, sometimes scabrous above; petioles slender, sometimes short or wanting. *Inflorescence* mostly a solitary head; peduncles elongate or almost wanting, sometimes stout, pubescent. *Heads* radiate; involucral bracts 4 or more, foliaceous, sometimes

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[43] Other synonyms are listed by Blake (1915: 197). Only the names noted here relate to Panamanian material.

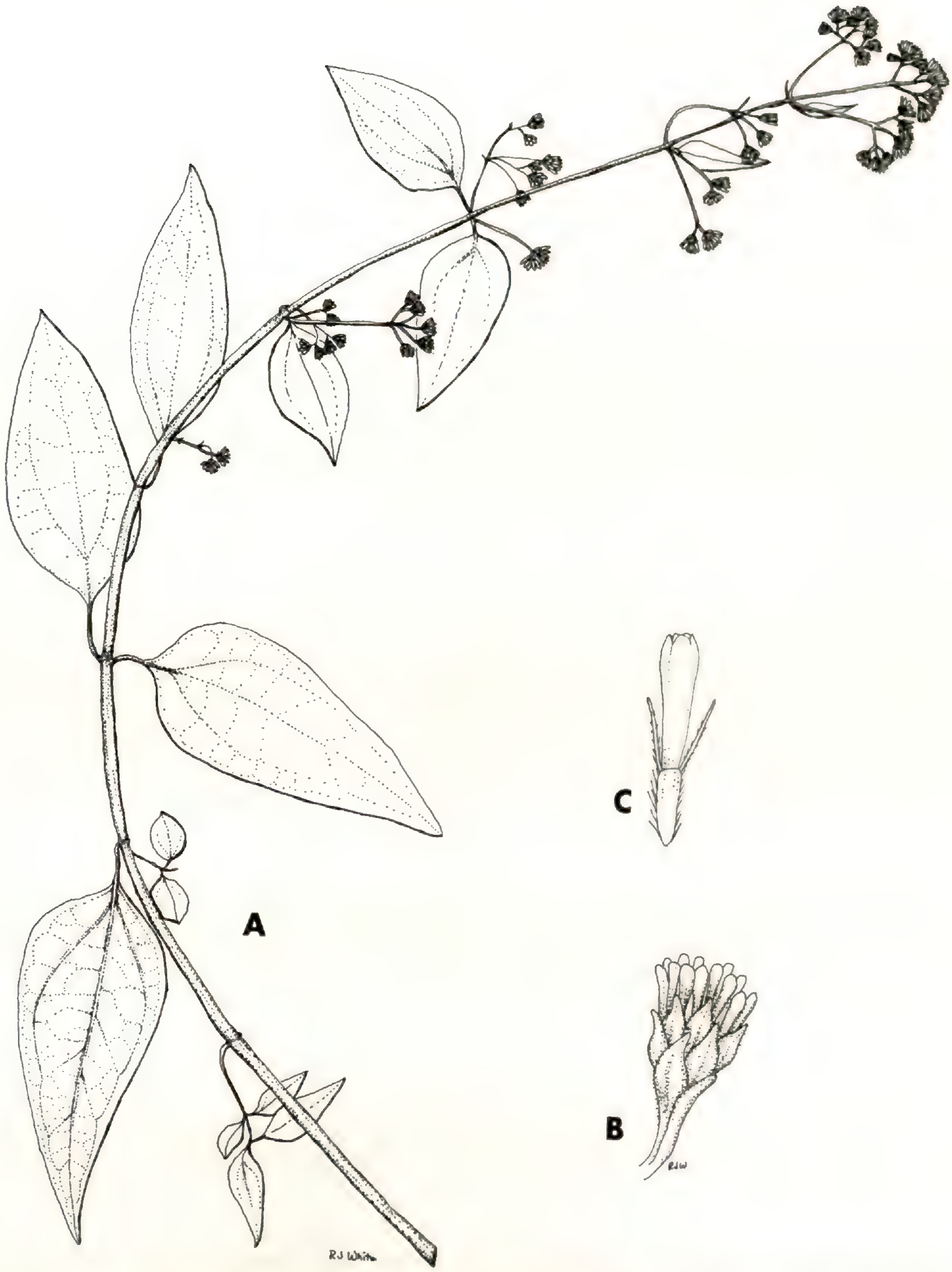

FIGURE 68. *Salmea scandens* (L.) DC.—A. Flowering branch (× ½).—B. Head (× 3½).—C. Floret (× 4). [After *Williams 284* (NY).]

apparently petiolate, eglandular, pubescent on both sides, rarely rudimentary; paleas tubular, the edges overlapped and fused below, the apex dentate or lobed, mostly pubescent, indurate, expanding and sclerifying in fruit; receptacle conical; ray florets 3–10, fertile, corolla yellow, the pubescent tube forming much of the

length, the limb elliptical with a conspicuously notched apex, ovary as long as the corolla tube, flattened, sterile; disc florets several to many, the corolla with elongate, slender, strigose apical lobes, the tube little differentiated, the stamens dark, exserted or not, the appendages narrow, long, dark, eglandular, the basal auricles small or indistinct, the style branches cylindrical, pilose, the style base expanded-globose, stipitate, the ovary turbinate, the pappus a ring of hairs or squamellae, or wanting, the carpopodium conspicuous. *Fruit* a utricle, the sclerified palea sometimes strongly oblique, often with a slender beak, fused to the achene apex.

A genus of about 8 species of warm temperate and tropical America, and one species (the type) of dry regions of Africa. *Sclerocarpus* may be recognized in flower by the elongate, strigose lobes of the disc florets and the elongate anther appendages, and in fruit by the distinctive oblique, urn-shaped utricles.

Bentham (1872) considered *Aldama* LaLlave & Lexarza to be synonymous. Although closely related, that genus is distinguished in having three distinctive types of floret per head. Feddema in his herbarium annotations recognized *Aldama* as distinct.

Literature:

Feddema, C. 1972. *Sclerocarpus uniserialis* (Compositae) in Texas and Mexico. Phytologia 23: 201–209.

1. **Sclerocarpus divaricatus** (Benth.) Hemsl., Biol. Centr. Amer., Bot. 2: 164. 1881.—Fig. 69.

Gymnopsis divaricata Benth., Bot. Voy. Sulphur 116. 1845. TYPE: Gulf of Fonseca (K, not seen).

Erect, spreading *herb* to 1.5 m tall; branches slender, divaricate; roots short and fibrous. *Leaves* alternate or at the base opposite, to 9 cm long, ovate, apically acuminate or acute, basally rounded, obtuse or cuneate, the margins serrate, sometimes saliently so, 3-nerved from near the base, scabridulous with copious, stiff, ascending hairs; petiole slender, 5–30 mm long, an intrapetiolar ridge mostly present below. *Inflorescences* solitary heads on slender, to 6 cm long, apically tomentose peduncles. *Heads* radiate; involucral bracts 4–5, ovate, foliaceous, mostly 6–11 mm long, apically obtuse, basally rounded, sessile, the margins entire, both sides grey-pubescent with ascending, appressed hairs; paleas slightly exceeding the ovary, enfolding the ovary and the edges connate to about halfway up, pilose, apically ca. 3-lobed, erose-pilose; ray florets several, the corollas yellow, ca. 20 mm long, the narrow, pilose tube forming ⅓ the length, the limb broadly ovate, apically 2–3-dentate, basally truncate, dorsally pubescent, ventrally uniform in color and texture, glabrous, the ovary sterile, pubescent, 2 mm long, pappus

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Figure 69. *Sclerocarpus divaricatus* (Benth.) Hemsl.—A. Habit (× ⅗).—B. Achene enfolded by involucral bract (× 5).—C. Disc Corolla (× 4). [After *Molina 22028*, Honduras (MO).]

A
B
C

wanting; disc florets numerous, the corolla 13–14 mm long, the tube not differentiated, cylindrical but broadening slightly upwards, hispid, especially on the upper portion, the apical lobes 3 mm long, strigose, the ventral hairs below the expanded apex black, the apices yellow, thick, slightly expanded, dorsally white-strigose, ventrally verrucose, the anthers dark, the thecae 2 mm long, the appendages narrowly lanceolate, 0.8 mm long, the bases obtuse or subauriculate, the style branches cylindrical, strigose, the style base expanded-globose, stipitate above the nectary, the ovary lenticular, glabrous, 1–1.5 mm long, dorsiventrally compressed, 2-nerved, the pappus wanting, the conical, glandular apex surmounted by a short cylindrical umbo and nectary, the carpopodium large. *Fruit* a globose-prismatic utricle, ca. 2 mm across, greenish or stamineous, the beak minute, apically tuberculate, sparingly white-pilose; achene reddish brown, faintly dark-striate, broadly turbinate, the base oblique; pappus wanting, the apex a hard, solid cylindrical peg, surmounted by a minute, cylindrical, disclike nectary; embryo broadly turbinate.

Superficially resembling a species of *Wedelia*, *Hymonostephium* or other yellow-flowered helianthoid Compositae, this species is highly distinctive upon closer examination and is unique in the Panamanian flora in a number of easily observed characters; the foliaceous involucre is approached only in species of *Montanoa* and *Rumfordia*; the ray corollas have unusually long tubes and are pilose on the dorsal surfaces; the disc corollas are not clearly differentiated into tube and limb, and the 5 apical lobes are strigose, ending in yellow, outcurving pads, highlighted by black hairs just below them; the anther appendages are dark like the thecae, and are narrowly lanceolate; both anther appendages and corolla lobes are proportionally much longer than in most other Panamanian species of Compositae. The fruit, a utricle formed of the achene enveloped by the palea is also unique. There is fusion between the palea and achene at the apex and basally at the carpopodium, a feature perhaps unique in the family. In some collections of this species from Mexico, the palea of some fruits on some heads is extended as a narrow ligule, but this could not be observed in the Panamanian collection. Because of the paucity of material from Panama, the above description is taken mainly from *Anderson & Mori 296*, Costa Rica (MO). *Sclerocarpus divaricatus* ranges from Mexico into South America.

CHIRIQUÍ: Ca. 3 mi above David on way to Boquete, *D'Arcy & D'Arcy 6300* (MO).

68. SIGESBECKIA

Sigesbeckia[44] L., Sp. Pl. 900. 1753; Gen. Pl., ed. 5. 973. 1754. TYPE: *S. orientalis* L.

Siegesbeckia sensu auct., not L.

Mostly erect, branching, annual *herbs*, a few species procumbent or scapose; stems mostly with erect, multicellular hairs, these often gland-tipped; roots mostly fibrous. *Leaves* opposite, simple, mostly ovate or elliptic, entire or serrate,

[44] For a list of synonyms see Humbles (1972). Only this name has been used for Panamanian material.

viscid-pubescent with weak, spreading multicellular, often gland-tipped hairs, the surface sometimes glandular; petioles mostly winged, sometimes basally auriculate or nearly connate-perfoliate, the leaves near the inflorescence smaller, sessile. *Inflorescence* an open, several–many-flowered panicle; peduncles with prominent multicellular, often glandular hairs; bracts foliaceous; unpaired, scale-like bractlets often present on the pedicels. *Heads* mostly radiate, small; involucral bracts of 2 dissimilar series, the 5 outermost lanceolate to linear-spathulate, apically rounded, mostly copiously stipitate-glandular, the stipes stout and the glands conspicuous, opaque, the innermost as many as the ray flowers, ovate, apically deltoid to acuminate, stipitate-glandular, enveloping the ovaries of the ray florets; paleas ovate, scarious, apically stipitate-glandular, enveloping the disc florets; receptacle conical, small; ray florets 5–15, rarely lacking, the corolla yellow, the tube forming half the length, sometimes cobwebby-pubescent, the limb broad, apically sinuate-dentate or bifid, the style branches short, the ovary fertile, asymmetrically fusiform-lenticular, the carpopodium somewhat ventral, pappus wanting; disc florets few to numerous, the corolla with the tube making up half the length, sometimes pubescent, the limb campanulate, angled with 5 deltoid lobes, the anthers yellow or green, with ovate, discrete-appearing apical appendages, basally auriculate, the filaments inserted high in the corolla tube, mostly not flexing in development or anthesis, the style branches somewhat flattened, cuneiform, dorsally pilose at the broadest point, the style base not expanded but articulated with the umbonate ovary apex, the ovary fertile, slightly compressed laterally with a prominent carpopodium, the apex conical with a cylindrical umbo; pappus wanting. *Achenes* black, minutely striate, curved, plump, sometimes strongly angled, square or ovoid in cross section; carpopodium indistinct; pappus wanting.

Sigesbeckia includes about 9 species of warm parts of both the New and Old Worlds. The glandular-stipitate, narrow outer series of involucral bracts are a good feature for recognition. The paleas become indurated in fruit, enveloping the achene but ultimately releasing it.

Literature:

Humbles, J. E. 1972. Observations on the genus *Sigesbeckia*. L. Ci. & Nat. 13: 3–19.

McVaugh, R. & C. Anderson. 1972. North American counterparts of *Sigesbeckia orientalis* (Compositae). Contr. Univ. Michigan Herb. 9: 487–493.

1. **Sigesbeckia jorullensis**[45] H.B.K., Nov. Gen. Sp. Pl. 4: 284. 1820. TYPE: Mexico *Bonpland*, (P).—FIG. 70.

Erect, short-lived branched *herb* to 1 m tall; stems drying striate, with spreading, multicellular, glandular hairs; roots fibrous. *Leaves* opposite, to 10 cm long (including petiole), apically acute, basally rounded or truncate, acuminate into the petiole, the margins serrate, the principal veins 3 from the base,

[45] For a list of synonyms see Humbles (1972). Only this name has been used for Panamanian material.

FIGURE 70. *Sigesbeckia jorullensis* H.B.K.—A. Habit (× 2/5). [After *White 45* (MO).]—B. Ray floret (× 7 2/5). [After *Fiebrig* 2068, Bolivia (MO).]

puberulent above and beneath with scattered, multicellular hairs, some of these gland-tipped, the surface eglandular; petiole prominently winged, basally expanded-auriculate and connate in pairs; leaves near the inflorescence much smaller, sessile with cuneate bases. *Inflorescence* an open, several–many-flowered panicle; peduncles slender, copiously glandular with erect hairs; bracts foliaceous; bractlets scalelike, not opposed. *Heads* small, inconspicuously radiate; outer involucral bracts 5, spreading, linear-oblanceolate, apically obtuse or rounded and slightly expanded, 8–18 mm long, ca. 1 mm wide, copiously stipitate-glandular, the inner 8 involucral bracts ca. 3 mm long, cucullate and enveloping the ray flower, apically acute or acuminate, 3-nerved, dorsally stipitate-glandular; paleas broadly ovate, scarious, enveloping the flower, the apex stipitate glandular; receptacle conical; ray florets 4–5 mm long, the corolla yellow, the cobwebby, apically glandular tube forming about half the length, the tube with an apical lobe opposite the ligule, the ligule recurved, broadly elliptical, 3-nerved, apically sinuate 3-dentate, the style branches darker than the style, the style base not expanded, the ovary fertile, 1.5 mm long, irregular-fabiform, glabrous or minutely cobwebby, the pappus wanting, the carpopodium relatively large; disc florets ca. 8, ca. 4 mm long, the corolla yellowish, ca. 2 mm long, the tube with erect hairs, forming half the length, the limb campanulate-angular, lobed ⅓–½ way down, the lobes deltoid, glabrous, the stamens inserted at the apex of the tube, the anthers green, the appendages ovate, the adjacent basal auricles connate, ?toothed, the style branches flattened, the basal half pilose, the apex deltoid, the style base not expanded, the nectary cylindrical, the ovary fabiform, glabrous, slightly compressed laterally, the apex a contracted umbo surmounted by the nectary. *Fruit* a utricle or achene, black, minutely striate, ca. 2 mm long, plump and the angles rounded, slightly beaked, sometimes falling enclosed by the palea; carpopodium inconspicuous; pappus wanting.

Sigesbeckia jorullensis is distinguished by the linear, stipitate glandular involucral bracts. Several features of the plants are of interest, e.g., the ligulelike corolla projection at the adaxial apex of the corolla tube, the inner series of involucral bracts which enfold the ray flowers much like paleas, and the insertion of the stamen filaments which at no stage flex in preparation for anthesis. The species ranges from southern Chile to northern Mexico and occurs on Hispaniola.

A related species, *S. agrestis* Poepp. & Engl., may be expected in Panama. It differs in its achenes being square rather than ovate in cross section, in its usually succulent stems, and in its usually shorter outer series of involucral bracts. *Sigesbeckia jorullensis* is a species of upper elevations; *S. agrestis* is a species of lowlands.

CHIRIQUÍ: 2.7 mi NW of Río Chiriquí Viejo, W of Cerro Punta, *Croat 22418* (MO). Bajo Chorro, Boquete District, 6000 ft, *Davidson 150* (GH). Cerro Pando, valley of the upper Río Chiriquí Viejo, *White 45* (MO).

69. SIMSIA

Simsia Pers., Syn. Pl. 2: 478. 1807. LECTOTYPE: *Coreopsis amplexicaulis* Cav. = *Simsia amplexicaulis* (Cav.) Pers.

?*Amania* Bert. ex. DC., Prodr. 5: 576. 1836. Based on *Hopkirkia fruticulosa* Spreng.
Barrattia A. Gray & Engelm., Proc. Amer. Acad. Arts 1: 48. 1846. TYPE: *B. calva* A. Gray & Engelm. = *Simsia calva* (A. Gray & Engelm.) A. Gray.
Encelia sect. *Simsia* (Pers.) A. Gray, Proc. Amer. Acad. Arts 19: 8. 1883.

Pubescent, branched, short-lived, erect *herbs*. *Leaves* opposite except near the inflorescence, mostly serrate, sometimes lobed, 3-nerved; petiolate with an interpetiolar ridge or auricles. *Inflorescence* loosely paniculate; peduncles elongate, ebracteolate. *Heads* radiate or discoid, subglobose; involucral bracts in about 3 series, imbricate, lanceolate, equal or not, sometimes alike, dorsally pubescent, 3–9-nerved, mostly indurate but often green; paleas scarious, stiff, acuminate, often pubescent upward, persistent, conduplicate and half-enfolding the flowers; receptacle flat or convex; ray florets several in 1 series, sometimes wanting, the corolla mostly yellow with a pubescent tube and an elliptical, emarginate limb, the androecium wanting, the style short and stout, the ovary sterile, trigonous, slender, often epappose; disc florets numerous, mostly yellow, the corolla with a short, pubescent tube and a cylindrical, 5-lobed limb, puberulent on the veins, slightly ventricose, the anthers with short appendages and usually stiff dorsal ascending hairs near the top of the connective, basally obtuse or subauriculate, the style branches slender, ascending-strigose, the style base expanded, elevated or (Robinson & Brettell) immersed in the nectary, the ovary fertile, laterally flattened. *Achene* flat, black, the margins thin but sometimes ciliate, the sides sometimes pubescent; pappus of 2 stiff, basally flattened, ascending-strigose bristles, rarely wanting.

Simsia includes perhaps 40 species ranging throughout tropical and warm temperate America. One species occurs in the Greater Antilles, and one species occurs in Panama. The relatively large, globose heads with numerous involucral bracts and the tomentose or velutinous leaves which usually dry dark gray-green are good features for recognition. The flat, black, 2-awned achenes are also distinctive.

Literature:

Robinson, H. & R. D. Brettell. 1972. Studies in the Heliantheae (Astereae). II. A survey of the Mexican and Central American species of *Simsia*. Phytologia 24: 361–377.

1. **Simsia panamensis** H. Robinson & Brettell, Phytologia 24: 372. 1972. TYPE: Panama, *Standley* 25386 (US, not seen).—FIG. 71.

Erect, branched *herb* to 3 m tall; stems slender, drying striate, puberulent with 1 mm long, 5–6-celled, spreading, deciduous hairs and short, often glandular hairs. *Leaves* opposite except near the inflorescence, thin, softly tomentose or velutinous on each side with long simple hairs and stipitate glands, ovate or elliptical, sometimes sublobate, apically acute, basally obtuse to cordate, the margins serrate, drying dark gray-green, 3-nerved from the base or nearly so; petioles slender, to 3 cm long, the nodes with a manifest intrapetiolar ridge. *Inflorescence* an open panicle, the branching alternate, and the nodes subtended

FIGURE 71. *Simsia panamensis* H. Robinson & Brettell—A. Habit (× 2/5).—B. Head (× 1⅔). [After *Blum 1866* (MO).]

by bracts which are smaller and narrower upwards. *Heads* radiate, subglobose, to 20 mm across, yellow; involucral bracts numerous in ca. 3 similar, imbricate series, lanceolate, 7–9 mm long, conspicuously 3–7-nerved, indurate but remaining at least partly dark green, dorsally pilose; receptacle convex; paleas scarious,

acuminate, dorsally pubescent upwards, sometimes mucronate, conduplicate and covering more than half of the floret; ray florets in 1 series, ca. 15 mm long, the corollas yellow, early deciduous, ca. 6 mm long, the tube pubescent, ca. 2 mm long, the limb elliptical, pubescent on the veins, emarginate, ca. 7 mm long, the ovary sterile, slender, 3-angled, glabrate, 5 mm long, epappose; disc florets numerous, 11 mm long, the corolla 6 mm long, the tube densely pubescent, the throat cylindrical, basally ventricose, the 5 lobes dorsally puberulent, the anthers yellow, ca. 3 mm long, with a few stiff ascending hairs arising near the apex of the connective, the appendages small, yellow, the base obtuse or subauriculate, the style branches elongate, ascending-pilose, the style base expanded-elliptical, elevated, the ovary laterally flattened with an apical stipe. *Achene* black, flat, 4 mm long, elliptical, the margins ciliate, the sides with a few hairs; pappus of two basally flattened strigose, stiff, 5 mm long awns.

This species may be recognized by its softly tomentose leaves, large size, globose yellow heads, and flat, black achenes. It is similar to *Simsia dombeya* DC. of Peru which differs in having achenes more than 6 mm long. Several species from neighboring areas, e.g., S. *polycephala* Benth. of Costa Rica may be conspecific, but no type material of these species has been seen. It differs from the similar S. *pubescens* Triana of South America in its narrower, pubescent involucral bracts. In Panama, most collections come from the Azuero Peninsula.

CANAL ZONE: Ancón Hill, *Greenman & Greenman 5109, 5119* (both MO). COCLÉ: Río Hato airstrip, *Burch et al. 1146* (GH, MO). Entrance to Río Hato air base, *Blum & Tyson 1866* (MO). Río Chico 4 mi W of Antón, *Tyson & Blum 2595* (MO). Near Penonomé, *Williams 242* (NY). HERRERA: Road from La Avena to outskirts of Pesé, *Burch et al. 1312* (GH, MO). 4 mi S of Los Pozos, *Tyson 2697* (MO). LOS SANTOS: 7 mi S of Chitré, *Croat 9699, 9703* (both MO). Salinas de Chitré, *D'Arcy & Croat 4165* (MO). Ca. 7 mi S of Chitré, *D'Arcy & Croat 4171* (MO). Headwaters of Río Pedregal, 25 mi SW of Tonosí, 2500–3000 ft, *Lewis et al. 2982* (MO). 17.8 mi S of Macaracas, 1100 ft, *Lewis et al. 1616* (MO, GH). Monagre Beach, 5 mi SE of Chitré, *Tyson et al. 3024* (MO). 12 mi S of Macaracas, *Tyson et al. 3069* (MO). PANAMÁ: Near San Carlos, *Allen 1131* (MO). Punta Paitilla, *Heriberto 222* (NY); *Piper 5427* (NY). Road to Cerro Azul, 1600 ft, *Tyson 6329* (MO).

70. SPILANTHES

Spilanthes[46] Jacq., Enum. Pl. Carib. 8. 1760. TYPE: S. *urens* Jacq.

Erect or prostrate ephemeral (Panama) *herbs*, sometimes rooting at the nodes; stems fistulose, glabrous or pubescent. *Leaves* opposite, entire or shallowly toothed, glabrous or pubescent with short, simple hairs, sometimes with sessile glands, mostly 3-nerved from near the base; petiolate or cuneate and sessile. *Inflorescence* one or a few heads arising terminally, axillary to a pair of leaves; peduncles slender, elongate, ascending, drying striate or angled. *Heads* yellow (Panama), white or purplish, radiate or discoid, at first lenticular, becoming globose or elongate-conical; involucral bracts slightly imbricate in 1–2 similar series, lanceolate, oblong or ovate, apically rounded or obtuse, sometimes mucronulate, or with a narrow hyaline margin, 1–several-nerved, the midvein often basally prominent;

[46] For synonyms of *Spilanthes*, see Moore (1907).

receptacle conical or fusiform; paleas oblong, folded around the florets; ray florets when present few, in 1–2 series, sometimes showy, the tube short-pubescent, slightly expanded basally, the limb broad, 2–3-sinuate-toothed, the androecium lacking, the style branches slightly exserted, resembling those of the disc florets but smaller, the style base slightly expanded, the ovary strongly 2–3-angled with a convex dorsal surface, otherwise resembling those of the disc florets; disc florets numerous, the corollas often colored, tubular and slightly expanded in the upper portion or campanulate, the (4–)5 deltoid lobes often oblique to the tangential axis of the head, papillose on the dorsal surface, the tube glabrate basally swollen, the stamens (4–)5, the anthers mostly dark with deltoid, infolded appendages and coherent adjacent auricles, the style branches flattened, marginally papillose or ciliate, apically truncate and fringed, the style base stipitate, much expanded and filling the expanded corolla base, the ovary laterally compressed, lenticular to flat, obovate in outline, apically recessed at the region of corolla insertion, with a small umbo below the stylar base. *Achene* black, the exocarp transparent, the margins thin to massively thickened, ciliate, the sides elevated or flat, glabrous, pubescent, or tuberculate, the endocarp black, finely striate; pappus of 2–several slender bristles or wanting.

Spilanthes is a genus of about 50 species of tropical and temperate regions of the New and Old World and is best represented in America and Africa. The black seed with fine perpendicular striae and the easily removed, sometimes tuberculate, exocarp are reminiscent of *Eleutheranthera*, but other features, including the general shape of the achenes, are quite different.

A number of writers have reported *Spilanthes uliginosa* Swartz from Panama but such Panamanian material is referrable to *S. alba* L'Her. *Spilanthes uliginosa* is smaller with narrower leaves. It is a species from the Greater Antilles.

Literature:

Koster, J. T. & W. R. Philipson. 1950. Nomenclatural changes in *Spilanthes* and *Blainvillea* with remarks and a key to the species of *Spilanthes* in the Malay Archipelago. Blumea 6: 349–354.

Moore, A. H. 1907. Revision of the genus *Spilanthes*. Proc. Amer. Acad. Arts 42: 521–569.

Standley, P. C. 1928. Flora of the Panama Canal Zone. Contr. U.S. Natl. Herb. 27: 1–416.

a. Achene margin massive, 4–10 cells wide on each side of the line of hairs; leaf apices obtuse or acute and mostly more than 3 cm long ..... 4. S. *paniculata*
aa. Achene margin thin, 1–2 cells wide on each side of the line of hairs; leaf apices acute or acuminate, if obtuse, then leaves less than 3 cm long.
  b. Ligules prominent, more than 8 mm long; receptacle more than 2 mm across at the base; heads becoming more than 8 mm across; upland plants ..... 3. S. *oppositifolia*
  bb. Ligules inconspicuous, less than 6 mm long; receptacle less than 1.5 mm across at the base; heads becoming less than 7 mm across; lowland plants.
    c. Trailing plants; leaves mostly more than 3.5 cm long; ligules ca. 2 mm long, little exserted from the involucral bracts ..... 2. S. *diffusa*
    cc. Erect plants; leaves less than 3 cm long; ligules ca. 3 mm long, exserted about the length of the involucral bracts ..... 1. S. *alba*

1. **Spilanthes alba** L'Her., Stirp. Nov. 7, *tab. 4.* 1784 (March, 1785). "*Spilanthus albus.*" TYPE: Peru, *Dombey*, (G-DC-holotype, not seen, IDC G-DC 962, III, 5. "h Dombey, Musee de Paris 1833"; P, isotype).—FIG. 72D.

Bidens ocymifolia Lam., Encycl. Meth. 1: 416. 1783 (August, 1785). TYPE: Cultivated in Paris, received from Dombey, Peru (BM, "L'Heritier").
Spilanthes radicans Jacq., Coll. 3: 229. 1789 (1791). TYPE: Cultivated in Vienna, received from Venezuela, not seen.
S. *exasperata* Jacq., Ic. Pl. Rar. 3: 15, *tab.* 584. 1795. Renaming of S. *radicans* Jacq.
S. *ocymifolia* (Lam.) A. H. Moore, Proc. Amer. Acad. Arts 42: 531. 1907.
S. *ocymifolia* f. *radifera* A. H. Moore, Proc. Amer. Acad. Arts 42: 533. 1907. TYPE: Colombia, *Smith 513* (NY, holotype, not seen; MO, isotype).

Erect, branched *herb* to 70 cm tall, sometimes rooting at the lower nodes; stems pilose with weak spreading hairs on emerging, soon glabrescent, often reddish, fistulose. *Leaves* opposite, ovate, to ovate-lanceolate, apically acuminate or rarely acute, basally obtuse or rounded, the margins entire or weakly serrate, glabrate; petiole 5–30 mm long. *Inflorescence* mostly a solitary head but sometimes a loose cluster of heads; peduncles slender, elongate, ascending and overtopping the leaves, to 9 cm long, glabrate. *Heads* 5–8 mm across, mostly radiate, becoming elliptical or conical, to 12 mm long; involucral bracts ca. 8, slightly imbricate, oblong, apically erose or mucronulate, the margins hyaline, the midvein darker than the lamina and basally impressed; receptacle fusiform, 5–7 mm long, basally 1 mm across; paleas stramineous, apically colored, enfolding the florets; ray florets few, inconspicuous, ca. 5 mm long, the corolla yellowish, ca. 3 mm long, the limb 3-nerved, apically truncate or obscurely 3-dentate, the tube ca. 1 mm long, pubescent on the 2 angles, the androecium wanting, the style branches drying dark orange, not evidently papillose, the style base expanded, stipitate above the ovary, the ovary strongly 3-angled, sparingly pubescent between the angles and sometimes inconspicuously tuberculate on the dorsal surface, otherwise resembling that of the disc florets; disc florets numerous, ca. 4 mm long, the corolla tubular, the 5 deltoid lobes oblique to the tangential axis of the head, papillose on the dorsal surface, the stamens 5, the anthers ca. 0.5 mm long with deltoid appendages and coherent adjacent basal auricles, the anther collar indistinct, the style branches yellow or orange, truncate and apically papillose-fringed, the style base globose, much expanded, the ovary laterally compressed, almost flat, obovate in outline with a small apical umbo below the style base. *Achene* black, 1.5 mm long, the pericarp transparent with a yellowish cast, the margins thin, long-ciliate, the testa black, shiny, finely striate; pappus of 2 weak bristles.

A species widespread in tropical America ranging from Mexico to Peru, *Spilanthes alba*, occurs in Panama as a weed of moist places at lower and middle elevations, and it appears to have some salt tolerance. Superficially much like *S. paniculata*, it is distinct in its thin achene margins, acuminate leaf apices, and longer disc corollas. The flower color is reported variously as yellow, yellowish-green, white, or greenish-white. This may be what Standley (1926) referred to as *S. uliginosa.*

CANAL ZONE: Barro Colorado Island, *Croat 7468, 7782* (both MO). Madden Dam, *Dwyer 3039* (MO). Chagres, *Fendler 166* (MO). Cerro Galera ca. 2 km from Pacific Ocean, 350–400 m, *Gentry 6656* (MO). COCLÉ: Below Cerro Pilón, *Croat 13460* (MO). El Valle de Antón,

FIGURE 72. *Spilanthes*.—A–B. S. *oppositifolia* (Lam.) D'Arcy.—A. Habit (× ½).—B. Head (× ½). [After *Partch 69-11* (MO).]—C. S. *paniculata* Wall. ex DC. Achene (× 7½). [After *Burch et al. 1059* (MO).]—D. S. *alba* L'Her. Achene (× 15). [After *Tyson 6440* (MO).]

1000–2000 ft, *Lewis et al. 2533* (MO). COLÓN: 6 mi SW of Portobelo, *Wilbur & Luteyn 11659* (MO). Agua Fria, ca. 8 mi N of Santa Fe, 50 m, *Duke 10106* (MO). HERRERA: Near Ocú, 100 m, *Allen 4046* (MO). LOS SANTOS: Monagre Beach, 5 mi SE of Chitré, *Tyson et al. 3054* (MO). 12 mi S of Macaracas, *Tyson et al. 3059* (MO). PANAMÁ: Taboga Island, *Allen 139* (MO). Road to Cerro Jefe beyond Goofy Lake, *Correa et al. 570* (MO, US). Isla del Rey, *Duke 9509* (MO). Isla Esperitu Santo, *Duke 10436* (MO). Road to Cerro Jefe, 2–3 mi S of Goofy Lake, 2000–2200 ft, *Lewis et al. 245* (MO, NY, US). SE slope of Cerro Campana, *Lewis et al. 3152* (MO). Cerro Campana, 2500 ft, *Tyson 6440* (MO). Ca. 9 km SE of El Valle de Antón, *Wilbur et al. 11167* (MO, US). VERAGUAS: 8 mi W of Santiago, *Tyson 6089* (MO).

2. **Spilanthes diffusa** Poepp. & Endlich., Nov. Gen. Sp. Pl. 3: 50. 1843. TYPE: Peru, *Poeppig 1206* (W, not seen, MO, photo).

Ceratocephalus diffusus (Poepp. & Endlich.) Kuntze, Rev. Gen. Pl. 1: 326. 1891.
Spilanthes ciliata var. *diffusa* (Poepp. & Endlich.) A. H. Moore, Proc. Amer. Acad. Arts 42: 539. 1907.

Prostrate or somewhat ascending, decumbent *herb*; stems glabrous to pilose. *Leaves* opposite, ovate, 7–25 mm long and 7–12 mm wide, apically obtuse or acute, basally rounded or short acuminate, the margins shallowly callose-serrate, glabrous to sparingly pubescent, reticulate veined beneath; petiole 2–3 mm long, mostly sparingly pubescent. *Inflorescence* one or two heads arising terminally, between a pair of leaves; peduncles 5–10 cm long, slender, ascending, glabrate, drying striate. *Heads* radiate, 4–6 mm tall, 7–10 mm across including ligules, becoming ellipsoidal or conical; involucral bracts ovoid, 2–3 mm long, short-ciliate, several ribbed; receptacle cylindrical-fusiform, ca. 10 mm long, 1 mm wide; paleas with streaks of orange-yellow, enfolding the florets; ray florets ca. 8, reportedly yellow but drying whitish, ca. 6 mm long, the ligule 3 mm long, 2 mm wide, apically 2–3-sinuate-dentate, the tube 2.5 mm long, pilose with ascending hairs outside, the style branches reduced, the style base expanded and discontinuous from the ovary, the ovary 3-angled, otherwise resembling that of the disc florets; disc florets numerous, ca. 3 mm long, the corolla tubular, 1.5 mm long, the lobes deltoid, somewhat oblique to the tangential axis of the head, minutely papillose on the dorsal surface, the tube glabrate, the anthers black, ca. 1 mm long with short-deltoid appendages and coherent adjacent auricles (?minutely tailed), the anther column little thickened, the filaments expanded below the collar, the style branches drying orange, apically truncate, the style base hemispherical, filling the corolla tube and stipitate above the ovary, the ovary laterally compressed, obovate in outline with a small umbo below the style base. *Achene* black, 1.5 mm long, lenticular, the exocarp transparent with a yellowish cast, the margins thin, long ciliate, the endocarp black, fine striate; pappus of 2–several weak bristles.

This species occurs sporadically in tropical America and is known in Panama from only two collections. It is distinct in its small, shortly but distinctly petiolate, blunt-tipped leaves and its trailing habit. It may not be distinct from species of the genus occurring in other areas, but it is distinct in the Panamanian flora. Assignment of the name S. *diffusa* to this taxon is not without question. The specimen of *Seibert 471* at Kew was annotated by A. H. Moore as S. *americana* (Mutis) Hieron.

COCLÉ: El Valle de Antón, 500–700 m, *Seibert 471* (K, MO). HERRERA: Ocú, *Ebinger 1052* (MO).

3. **Spilanthes oppositifolia** (Lam.) D'Arcy, comb. nov.—FIG. 72A–B.

Anthemis americana Mutis ex L.f., Suppl. Pl. 378. 1781, not *A. americana* L., Sp. Pl. 895. 1753. TYPE: Colombia, *Mutis* (LINN 1016.32).
A. oppositifolia Lam., Encycl. Meth. 1: 576. 1783 (1785). TYPE: not seen.
Spilanthes americana (L.f.) Hieron in Sodiro, Bot. Jahrb. Syst. 29: 42. 1901 (1900).
?*S. macrophylla* Greenman, Proc. Amer. Acad. Arts 39: 109. 1903. TYPE: Costa Rica (not seen).

Erect or sprawling branched *herb* to 1 m tall; stems pilose with weak spreading hairs, mostly glabrescent, often reddish, the lower nodes with a prominent interpetiolar ridge, fistulose. *Leaves* opposite, ovate to ovate-lanceolate, apically acuminate or occasionally acute, basally obtuse or rounded, to 10 cm long, entire or weakly serrate, glabrate; petiole to 3.5 cm long, apically narrowly winged. *Inflorescence* one or two heads arising terminally between a pair of leaves; peduncles slender, to 15 cm long, weakly ascending, glabrate. *Heads* radiate, 9–15 mm across exclusive of ligules, becoming ellipsoidal and then conical, to 15 mm long; involucral bracts ca. 8, slightly imbricate, 5–6 mm long, oblong or lanceolate, apically erose, the margins hyaline, the midvein basally prominent, other venation indistinct; receptacle narrowly conical or fusiform, 7–10 mm long, basally 3 mm across; paleas stramineous, enfolding the floret, apically yellow; ray florets few, ca. 15 mm long, the corolla showy yellow, the ligule 4–5 mm wide, apically 2-dentate, the tube ca. 3 mm long, sparingly pilose outside, the androecium wanting, the style branches like those of the central florets but shorter, the style base only slightly expanded, discontinuous from the ovary, the ovary 3-angled, otherwise resembling that of the disc florets; disc florets numerous, 4–5 mm long, the corolla tubular-campanulate, the 5 deltoid yellow lobes oblique to the tangential axis of the head, minutely papillose-grandular on both sides, the tube glabrate, basally expanded and inserted into the ovary apex, the anthers black, 1–1.2 mm long, with short-deltoid, infolded, apical appendages and coherent adjacent basal auricles, the style branches flattened, marginally papillose, truncate and apically papillose-fringed, the style base hemispherical, much expanded and discontinuous from the ovary, the ovary laterally compressed, flat to lenticular, obovate in outline with a small apical umbo below the style base. *Achene* black, 2 mm long, the exocarp transparent with a yellowish cast, the margins thin, long ciliate, the endocarp black, shiny, finely striate; pappus wanting.

Spilanthes oppositifolia is widespread in temperate and tropical America ranging from Missouri and the Carolinas on the north at least as far south as Catamarca in Argentina. A number of varieties have been proposed but the range of variability of *S. oppositifolia* and the taxonomy of its close relatives are not sufficiently understood to recognize infraspecific taxa at present. In Panama the species is known only in the Chiriquí mountains. It is distinct from other Panamanian members of the genus in the large size of the flower heads and ligules.

Selection of the name used here is based on the synonymy presented by Moore (1907).

CHIRIQUÍ: Nueva Suiza, *Croat 13503* (MO). N of Audubon Cabin, *Croat 13630* (MO). Above Boquete, 5200 ft, *D'Arcy & D'Arcy 6376* (MO). Above Cerro Punta on slope of Cerro Respinga, 8000 ft, *D'Arcy & D'Arcy 6523* (MO). Bajo Chorro, Boquete District, 6000 ft. *Davidson 148* (MO). Río Chiriquí Viejo N of Volcán City, 5200–5600 ft, *Duke 9017* (MO). Mountains N of Cerro Punta, *King 5302* (US). Along Río Caldera S of El Boquete, 1250 m, *Killip 3612a* (US). Alto Linio, 4000 ft, *Maurice 878a, 893* (both US). Nueva Suiza, *Partch 69-11* (MO). Cerro Punta, 5500 ft, *Sawyer 1967* (MO). Bajo Mona, mouth of Quebrada Chiquero along Río Caldera, 1500–2000 m, *Woodson et al. 1002* (MO).

4. **Spilanthes paniculata** Wall. ex DC., Prodr. 5: 625. 1836. TYPE: not seen.—FIG. 72C.

Ascending *herb* to 40 cm tall, sometimes rooting at the lower nodes; stems often reddish on emerging, with weak, spreading white hairs or glandular trichomes, soon glabrescent. *Leaves* opposite, ovate, 1.5–7 cm long, apically obtuse to acute but seldom acuminate, basally rounded or truncate, shallowly serrate, sparingly pubescent with spreading white hairs; petioles 4–30 mm long. *Inflorescences* of single or paired, ascending heads on slender peduncles mostly overtopping the foliage. *Heads* 6–8 mm across, radiate, becoming elliptical or conical, to 12 mm long; involucral bracts several, slightly imbricate, 3–5 mm long, oblong or ovate, marginally erose or entire, apically acute, obtuse or rounded-erose, several-nerved, a pair of elevated indurated lines often flanking the depressed midvein; ray florets few, inconspicuous, 4–5 mm long, the corolla yellowish, ca. 3 mm long, the limb as broad as long, apically 2–3-sinuate-dentate, the tube pubescent, ca. 1 mm long, the style branches yellowish, the style base slightly expanded, stipitate above the ovary, the ovary with two prominent angles and the dorsal surface strongly convex, otherwise resembling that of the central flowers; disc florets numerous, ca. 3 mm long, the corolla campanulate, 1.5–2 mm long, the 5 lobes slightly oblique to the tangential plane of the flower and conspicuously papillose on the dorsal surface, the tube indistinct, glabrous, basally expanded and inserted into the depressed ovary apex, the anthers ca. 0.8 mm long, the appendages deltoid, infolded, the adjacent auricles coherent, narrow, the anther collar thicker than the filament, the style branches flattened, sometimes not papillose on the margins, apically truncate, papillose, the style base globose, stipitate above the ovary. *Achene* 2 mm long, compressed-lenticular, ovate in outline, the pericarp transparent, massively thickened and ciliate at the margins, sparingly pubescent and tuberculate on the sides near the apex, endocarp black, shiny, finely striate; pappus of 2–3 weak, minutely strigose awns, sometimes wanting.

A species widespread in warm portions of the Old World, *Spilanthes paniculata* occurs in Panama as a weed of lowland towns and ruins. It also occurs in Bolivia at middle elevations. Superficially much like *S. alba*, this species is distinct in a number of inconspicuous details, including the less sharply pointed leaf apices, the shorter and broader corollas of the florets, and the thicker achene with its massively thickened margins.

CANAL ZONE: Fort San Lorenzo, *Burch et al. 1042* (MO, NY); *Porter et al. 5010* (MO); *Tyson & Blum 3699* (MO). DARIÉN: Around El Real, *Burch et al. 1059* (MO). Río Pirre, 2–5 mi above El Real, *Duke 4901* (MO). Río Pirre, ca. 10 mi S of El Real, *Duke 5411* (MO).

71. TITHONIA

Tithonia Desf. ex Juss., Gen. Pl. 189. 1789. Based on Desf., Ann. Mus. Natl. Hist. Nat. 1: 49, *tab. 4.* 1802 (delivered 1780). TYPE: *T. tagetiflora* Desf. = *T. rotundifolia* (Miller) Blake.

Mirasolia (Schultz-Bip.) Benth. & Hook.f., Gen. Pl. 2: 367. 1873. TYPE: *Tithonia calva* Schultz-Bip.

Urbanisol Kuntze, Rev. Gen. Pl. 1: 370. 1891. TYPE: *U. tagetiflorus* (Desf.) Kuntze = *Tithonia rotundifolia* (Miller) Blake.

Large *herbs* or *shrubs*, glabrate to scabrous or villous-sericeous, mostly sprawling or wide-branching. *Leaves* alternate, sometimes opposite below, simple, entire or 1–4-arcuate-lobed, the margins sometimes crenate or irregularly denticulate, mostly apically acuminate or acute, basally narrowed or rarely sessile, scabridulous to villous, the petiole base sometimes expanded and auriculate or decurrent on the stem. *Inflorescence* an undifferentiated panicle-like group of terminal heads, rarely solitary; peduncles elongate, apically expanded and fistulose, drying striate, sometimes with one or more foliaceous bracts along the length. *Heads* large and showy, radiate; involucral bracts in several equal or unlike series, indurated and many nerved, the innermost series rounded, obtuse or short acuminate; paleas hyaline, exceeding the achenes and completely enfolding them; ray florets several in one series, the ligules yellow or orange, elongate, 1–4-denticulate, dorsally puberulent, glabrous inside, the style and staminodes mostly wanting, the ovary abortive, flat or slightly triquetrous, often glabrous; disc florets numerous, 5-merous, the corollas tubular, puberulent outside, the teeth cuculate, colored with thickened margins and tomentose outside, basally contracted, the anthers black, the appendages yellow, expanded, cordate, somewhat infolded, the thecae connate, basally auriculate, the filaments flattened, puberulent, inserted low in the corolla tube, the ovary fertile, the style branches flattened, apically delineated from the appendage by a tuft or row of dorsal hairs, the style base sometimes a much enlarged bulb, slightly immersed in the nectary, the nectary peltate-cupuliform, the margin irregular, smooth. *Achene* compressed, obconical, gray or black, glabrous or pilose; carpopodium oblique, conspicuous or not; pappus wanting or (in our species) of two stout, persistent awns and a series of broad, apically erose scales.

The two species present in Panama are recognizable by their large aspect, showy flowers, lobed, scabridulous leaves, and by their mostly flattened, greyish, pilose achenes bearing awns and scales. One of these two species is widely grown for ornament and is naturalized in many tropical countries. The genus is native to tropical Mexico, Central America, and the Antilles and comprises about a dozen species. At least two elements are present in this genus; a group including those in Panama with pilose achenes with well-developed pappus and inconspicuous carpopodium, and a group with glabrous, often mottled achenes lacking pappus and having enlarged carpopodia. Species of both groups are present in Costa Rica.

Literature:

Blake, S. F. 1921. Revision of the genus *Tithonia*. Contr. U.S. Natl. Herb. 20: 423–436.

a. Outer involucral bracts less than half as long as the inner bracts, the outer bracts ovate, apically obtuse or short acuminate; ligules 4–5 cm long ..... 1. *T. diversifolia*
aa. Outer involucral bracts about as long as the inner bracts, the outer bracts acute; ligules 2–3 cm long ..... 2. *T. rotundifolia*

1. **Tithonia diversifolia**[47] (Hemsl.) A. Gray, Proc. Amer. Acad. Arts 19: 5. 1883.

Mirasolia diversifolia Hemsl., Biol. Centr. Amer., Bot. 2: 168, *tab. 47*. 1881. TYPE: not seen.

Large, shrublike *herb* to 2 m tall; stems drying green, striate, puberulent. *Leaves* alternate, ovate, or cuneiform, apically acuminate or acute, basally acuminate, entire and 2–3-lobed, the lobes acute with broad, rounded sinuses, the margins often crenate, darker and scabriduous above with short, stout, hairs, some with multicellular bases, beneath glandular and with weak white rugose hairs; petiole slender, basally clasping, often auriculate. *Inflorescence* of solitary or clustered terminal heads on elongate, apically expanded, striate, puberulent peduncles 8–15 cm long. *Heads* radiate, large and showy; involucre 25–40 mm across, the bracts in several series of at least 2 different sizes, broadly ovate and prominently veined, the outermost to 10 mm long, apically short acuminate or acute, the innermost twice as long, apically acute, obtuse or rounded; paleas hyaline, completely enclosing the ovary; ray florets several in one series, the ligules 4–5 cm long, apically 2–3-dentate, puberulent outside, drying with conspicuous nerves, the tube 2 mm long, the ovary abortive, 4 mm long, triquetrous, pilose, with a well-developed pappus; disc florets numerous, ca. 15 mm long, the corolla tubular, pubescent outside, the lobes yellow, narrowly obtuse with thickened, dorsally pubescent margins, the anthers black, 5 mm long, the apical appendages yellow, expanded and slightly enfolded, the basal auricles connate, the filaments flattened, ventrally puberulent, the ovary fertile, the style branches flattened, pubescent on both sides and tomentose dorsally at the base of the narrow appendage, the style base bulbous, 0.5 mm across, the nectary stipitate, crateriform, enclosing the base of the stylar bulb. *Achene* body 5 mm long, flat, somewhat triquetrous, the endocarp blackish, appearing grey under the dense ascending white indumentum; carpopodium inconspicuous; pappus of two sturdy, persistent, 5 mm long awns and a ring of broad, 2–3 mm long, distinct scales.

The broad involucral bracts of widely differing sizes distinguish this species from *Tithonia rotundifolia*. Cultivated for ornament, it occurs naturally in several parts of Panama. It is native to Mexico and Central America and is naturalized in many other tropical countries.

COCLÉ: Near El Valle de Antón, *Croat 13296* (MO). El Valle, 2000 ft, *Tyson & Godfrey 2467* (US). PANAMÁ: Between Chorrera and Capira, *Tyson 6427* (MO, NY).

2. **Tithonia rotundifolia** (Miller) Blake[48], Contr. Gray Herb. 52: 41. 1917.—Fig. 73.

Tagetes rotundifolia Miller, Gard. Dict., ed. 8. 1768. TYPE: Chelsea Garden, *Miller* (BM).

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[47] For a list of synonyms see Blake (1921). Only the listed names have been used for Panamanian material.

[48] For a list of synonyms see Blake (1921). Only the listed names have been used for Panamanian material.

Large, shrublike, short-lived *herb* to 4 m tall; stems drying green or brown, striate, puberulent. *Leaves* to 35 cm long, ovate or cuneiform, sometimes broadly so, apically and basally acuminate, entire or 3–5-lobed, the lobes ovate with obtuse sinuses, the margins mostly crenate, scabridulous above with short stout hairs and occasional glands, softly pubescent beneath with stout, arching, verrucose hairs; petiole elongate, winged in the upper portion, basally clasping the stem. *Inflorescence* of solitary or clustered terminal flowers on elongate apically expanded, striate, puberulent peduncles 8–20 cm long with one or more large or small foliaceous bracts along their length. *Heads* large and showy, radiate; involucral bracts 20–30 mm across, in several subequal series, 10–15 mm long, indurated, many nerved, whitish puberulent, the outermost slightly longer, acute, the innermost obtuse or short acuminate; paleas hyaline, dorsally puberulent, completely enclosing the achene; ray florets several in one series, the ligules yellow or orange, 2–3 cm long, minutely 1–2-notched, puberulent outside, drying with conspicuous veins, staminode sometimes present, the ovary abortive, ca. 3 mm long, flat but faintly 3-angled, glabrous, the pappus of scalelike awns and a ring of short hairs; disc florets numerous, ca. 10 mm long, the corolla tubular, pubescent on the veins outside, the lobes yellow, cuculate with the thickened margins, dorsally papillose-pubescent, the anthers black, 4 mm long, the appendages yellow, expanded and slightly enfolded, the basal auricles connate, the filaments flattened, minutely puberulent, the ovary fertile, the style branches flattened, ventrally puberulent with a tuft of hairs at the base of the short, narrow appendage, the style base slightly expanded, the nectary stipitate, crateriform with irregular margins, enclosing the base of the style. *Achene* body 5–6 mm long, flat, the endocarp blackish, appearing gray under the weak, white, ascending indumentum; carpopodium inconspicuous; pappus of two sturdy, persistent 3–5 mm long awns and a ring of broad, distinct, 2–3 mm long scales.

The acute outer involucral bracts which equal or slightly exceed the inner series are a good feature distinguishing this species from the larger-flowered, longer-lived *Tithonia diversifolia*. It is a native of Central America and the Antilles and has the widest native range of any member of the genus.

CHIRIQUÍ: 1 km W of La Repressa, Quebrada Guanabanito, *Busey 477* (MO). COCLÉ: 10 mi E of Natá at Río Grande, *Tyson 5218* (MO). HERRERA: Near Chitré, *Allen 1106* (MO). PANAMÁ: Isla Taboga, *Allen 1286* (MO). 3 mi beyond turnoff to Cerro Azul, *Croat 13008* (MO). Hills between Capira and Potrero, 80–130 m, *Dodge & Hunter 8647* (MO). Cerro Azul, *Dwyer 2182* (MO). Road to Cerro Azul, 500 ft, *Tyson 6330* (MO).

72. VERBESINA

Verbesina L., Sp. Pl. 90. 1753; Gen. Pl., ed. 5. 384. 1754. TYPE: *V. alata* L.

Herbs, *shrubs* or *trees*, rarely prostrate; stems glabrous or pubescent, in some species 2–6-winged by concaulescence of the petiole bases. *Leaves* alternate (in Panama) or opposite, dentate or lobed, rarely entire, mostly pubescent, sometimes scabrous; petioles sometimes winged or auricled, sometimes fused in part with the stem and forming wings. *Inflorescences* mostly several–many-headed, mostly open panicles; bractlets mostly minute, situated along the length or subtending

FIGURE 73. *Tithonia rotundifolia* (Miller) Blake.—A. Habit (× ½). [After *Tyson 5218* (MO).]—B. Head (× ½). [After *Tyson 6427* (MO).]

the heads and resembling involucral bracts. *Heads* large or small, mostly radiate, of various shapes; involucral bracts narrow in 2–6 graduated, more or less similar series, mostly much shorter than the paleas, the outermost bracts rarely the longest; paleas mostly resembling the involucral bracts but narrower and longer, the

apices various, enfolding the disc florets; ray florets mostly yellow or white, the limb broad, denticulate, the tube relatively long, often pubescent, the ovary mostly fertile, laterally compressed; disc florets numerous, the corolla tubular, 5-merous, the tube short and mostly poorly demarcated from the limb, the anthers appendaged, basally obtuse or auriculate, the style branches dorsally pubescent, sometimes apically penicillate with a short or long, deltoid, pubescent apical appendage, the two stigmatic lines often evident, the style base sometimes expanded, sessile on the cylindrical nectary, the ovary mostly fertile, ciliate, pubescent or glabrous, laterally compressed, lenticular, the pappus mostly of two, sometimes unequal, strigose awns. *Achenes* mostly black and broadly winged with two apical, strigose awns, the body or wings sometimes pubescent, the body sometimes tuberculate, the outermost achenes sometimes distinctive.

A commonly represented but poorly understood American genus of more than 100 species, *Verbesina* is distinguished by its compressed, winged achenes with their two apical awns. The ovary is usually stipitate. Several attempts have been made to segregate various elements into distinct genera, but these have not been accepted, and in the current century, little has been done to clarify the taxonomy of the group as a whole. In Panama, all species are shrubs or trees with alternate leaves, and the involucral bracts are short and narrow in 2–3 series.

a. Leaves mostly lobed.
  b. Stems glabrate ..... 2. *V. gigantea*
  bb. Stems copiously pubescent.
    c. Stems in inflorescence area winged by concaulescent petiole bases; leaves scabridulous above ..... 7. *V. turbacensis*
    cc. Stems not winged, or if so, only below the inflorescence area; leaves strongly scabrous above ..... 6. *V. sublobata*
aa. Leaves denticulate or entire, not lobed.
  d. Leaves scabrous above ..... 6. *V. sublobata*
  dd. Leaves glabrate above.
    e. Heads more than 10 mm across; leaves large, more than 20 cm long and 5 cm wide ..... 1. *V. fuscasiccans*
    ee. Heads less than 10 mm across (excluding rays); leaves smaller, narrower.
      f. Involucral bracts acute; leaf midvein glabrous beneath ..... 3. *V. guatemalensis*
      ff. Involucral bracts obtuse or rounded; leaf midvein puberulent beneath.
        g. Involucral bracts less than 3 mm long; disc corollas glabrous; pubescence of young stems all appressed ..... 5. *V. oerstediana*
        gg. Some involucral bracts more than 3 mm long; disc corollas basally pilose; young stems with some loose, spreading hairs ..... 4. *V. lanata*

1. **Verbesina fuscasiccans** D'Arcy, Phytologia 30: 6. 1975. TYPE: Panama, *Croat 27091* (MO).

Shrub to 2.5 m tall; stems stout, soft, finely striate, tomentose, glabrescent, light brown or yellowish. *Leaves* alternate, oblanceolate or obovate, to 30 cm long, 10 cm wide, apically short acuminate, basally acuminate into the winged petiole, the margins entire or denticulate, slightly revolute, veins ca. 9 on each side of the midvein, excurrent and contrasting beneath, less prominent above, glabrate, sparingly pubescent on the veins beneath, shining above, drying dark brown or green and contrasting with the stem; petioles 5–6 cm long, broadly winged, abruptly contracted at the very base. *Inflorescence* a condensed, cymose panicle

to 15 cm across, foliose bracts distributed through the branches; pedicels short or long (to 9 cm long), tomentulose with short, weak hairs. *Heads* ca. 2 cm across, globose; involucral bracts numerous, of two distinct forms, the outer series in 2–3 whorls, oblong, costate, ciliolate, with slightly expanded, green, rotund tips, the inner series in about 1 whorl, slightly longer, narrower, apically acute; paleas ca. 10 mm long, folded around the floret, the costa extended in a thin, ciliate wing, apically dark and the acute tip slightly outcurving; ray florets several, the corolla ca. 10 mm long, the tube tomentose, curved, the ligule narrow, apically entire or cuculate, the style branches linear, pubescent, the ovary fertile, laterally flattened, the margins corneous-ciliate, in part narrowly winged; disc florets numerous, ca. 11 mm long, the corolla shallowly lobed, ca. 7 mm long, the tube narrow, the base of the limb abruptly expanded, the anthers black, ca. 3 mm long, the appendages black, the basal auricles crumpled, the style branches fusiform, pubescent, the base expanded into a cylinder emersed in the urceolate nectary, the ovary fertile, flattened, ciliate but otherwise glabrous. *Achene* black, 5 mm long, flat, apically recessed, the margins ciliate and narrowly winged; carpopodium not evident; pappus of two short, stout strigose awns.

This species is distinctive in its large leaves which dry dark, contrasting with the light colored stems, in the nectary on the ovary which is large and urceolate, and in the ciliate margins of the achenes. The achene (immature in all material seen) resembles achenes of *Spilanthes*. It is likely that these margins expand and become broad wings with maturity.

Verbesina fuscasiccans is known only from two collections taken on Cerro Jefe, a hill northeast of Panama City.

PANAMÁ: E slope of Cerro Jefe, 2700 ft, *Blum & Dwyer 2189a* (MO). Campo Tres beyond Cerro Jefe, 700 m, *Croat 27091* (MO).

2. **Verbesina gigantea** Jacq., Coll. 1: 53. 1787; Ic. Pl. Rar. 1: 17, *tab. 175*. 1784.
TYPE: not seen.

V. myriocephala Schultz-Bip. in Klatt, Leopoldina 23: 144. 1887. TYPE: Mexico, *Liebman 271* (C, not seen, US, fragment, MO, photo).

Erect, branched *herb* to 3.5 m tall; twigs strongly angled and pubescent, soon glabrate, terete and finely striate. *Leaves* alternate, to 20 cm long, often 3–7-lobed more than halfway, the margins often minutely callose-denticulate, darker and sometimes scabridulous above, softly tomentose beneath, the venation elevated and reticulate beneath; petiole broadly winged to the base, basally auricled. *Inflorescence* a large, many-headed cymose panicle to 30 cm across; peduncles and rachis puberulent, soon glabrescent, sharply angled when young, soon terete and finely striate; bracteoles linear, those near the heads minute, scalelike, resembling the bracts of the involucre. *Heads* mostly radiate, small, 6–7 mm tall, 4–5 mm across; involucral bracts in 2–3 graded series, appressed, ciliate, dorsally pubescent, apically acute; paleas enfolding the flowers, scarious, apically acute, pubescent; ray florets few, ca. 7 mm long, the corolla limb deeply lobed, the tube pilose, the ovary ciliate, laterally compressed, stipitate, the pappus of two strigose awns; disc florets ca. 6 mm long, tubiform, the limb glabrous, the tube

pilose, constricted medially, the anthers auriculate, dark, the appendages dark, the style branches slender, minutely appendaged, the style base slightly expanded, sessile on a large, orange nectary, the ovary stipitate-fusiform, laterally compressed, ciliate, the pappus of two awns as long as the corolla tube. *Achene* body black, 5 mm long, with scattered brownish hairs, not tuberculate, broadly winged; pappus of two strigose awns ca. 2 mm long.

This species is similar to *Verbesina turbacensis* but may be distinguished by its glabrate unwinged stems and auricled leaf-bases. "Cerbatana."

CANAL ZONE: Ca. 4 mi S of Fort Sherman, *Blum & Tyson 2012* (MO). Near W end of Gatún Lake dam, *Blum & Tyson 1979* (MO). Barro Colorado Island, *Croat 4387* (MO). Road C21 near Police Lodge, *Croat 12994* (MO). Balboa Heights, *Greenman & Greenman 5029* (MO). Ancón Hill, *Greenman & Greenman 5111* (MO). Near Corozal, *Greenman & Greenman 5190* (MO). 2 mi N of Paraíso, *Lazor & Blum 5230* (MO). Between Corozal and Ancón, *Pittier 2164* (NY, US). Barro Colorado Island, *Shattuck 399* (MO); *Wetmore & Abbe 117* (MO). COCLÉ: Road to El Cope from Interam. Hwy., *Burch et al. 1371* (MO, NY, US). COLÓN: Santa Rita, 200–300 m, *Gómez-Pompa et al. 2979* (MO). PANAMÁ: Cerro Azul, *Croat 13025* (MO). Tocumen Airport, *Dwyer 1967* (MO). Goofy Lake to ca. 9 mi S toward Cerro Jefe, *Dwyer 7051, 7058* (both MO). SE slope of Cerro Campana, *Lewis et al. 3137* (MO, NY). Cerro Jefe, 2700–3000 ft, *Tyson et al. 3325* (MO). Road from Cerro Azul to Cerro Jefe, 2400 ft, *Tyson 6319* (MO).

3. **Verbesina guatemalensis** B. L. Robinson & Greenman, Proc. Amer. Acad. Arts 34: 550. 1899. TYPE: Guatemala, *Donnell Smith 2860* (GH, not seen).

Herb or weak *shrub* to 2.5 m tall; stems soft, finely striate, sometimes with conspicuous, elongate lenticels, soon glabrate, unwinged. *Leaves* alternate, lanceolate or oblanceolate, subentire, the margins sometimes irregularly sinuate, apically acute or acuminate, basally narrowed to the base, darker above and scabridulous, punctate with short white hairs, the lateral venation not prominent, beneath velutinous with small verrucose hairs; petiole wanting, auricles rotund, small but manifest. *Inflorescence* a many-headed, flat-topped, open panicle to 30 cm across; bracts becoming spatulate upwards, the bractlets linear, variously situated but sometimes subtending the head and resembling involucral bracts; peduncles angled, pubescent. *Heads* radiate or discoid, to 9 mm long (in Panama); involucral bracts appressed, ciliate, to 6 mm long, indurate and cuculate below, the apex acute or acuminate, sometimes slightly expanded or reflexed; paleas ca. 6 mm long, folded over the disc florets, ciliate on the keel and apex; ray florets few, the corolla white, rectangular, 3 mm long, 3-nerved, truncate, 3-lobed, the tube ca. 2 mm long, pilose, the ovary laterally compressed, pyriform, the narrowed basal portion forming a stipe, ciliate, with two short, strigose awns; disc florets 20–25, 5–6 mm long, the corolla 3–4 mm long, the basal ⅔ pilose, the tube not demarcated from the 5-lobed limb, the anthers black, the appendages dark, the style branches not expanded, apically appendaged, dorsally pubescent, the style base not expanded, subsessile on the ellipsoidal, 0.5 mm long nectary, the ovary laterally compressed, ciliate on the angles, the awns half as long as the corolla, slightly unequal. *Achene* body (Robinson & Greenman) 5 mm long, tuberculate, especially along the prominent midnerve; pappus awns 2, long, slender, equal.

This species is similar to S. *gigantea* but the leaves are not lobed. The heads of the single Panamanian collection are somewhat smaller than those seen from Nicaragua and Honduras.

CANAL ZONE: Road K-10D N of Arraiján, *Croat 15133* (MO).

4. **Verbesina lanata** B. L. Robinson & Greenman, Proc. Amer. Acad. Arts 34: 558. 1899. TYPE: Guatemala, *Tuerckheim 1344* (MO, US).

Shrub or *tree* to 4 m tall; twigs stout, tomentose with elongate, ascending, mostly appressed, yellowish brown hairs. *Leaves* alternate, elliptic or lanceolate, acuminate at both ends, veins 6–7 on each side of the midvein, conspicuously elevated and fine-reticulate beneath, glabrescent above, pilose beneath, tomentose on the veins, drying with a dusty brown appearance; petioles stout, 1–5 mm long, narrowly winged but more or less distinct from the blade. *Inflorescence* a large, many-headed flat- or round-topped panicle; rachis and peduncles stout, tomentose, drying brown; bracteoles linear, small, variously situated. *Heads* globose, ca. 7 mm long, radiate; involucral bracts in about 2 unequal series, the innermost ca. 4 mm long, evenly appressed pilose over the dorsal surface, not conspicuously ciliate; paleas resembling the involucral bracts but longer; ray florets ca. 8, the corolla yellow, the limb 4–6 mm long, dorsally pubescent in the basal half, dentate, the tube pilose, 1–2 mm long, the ovary laterally flattened, 1.2–1.5 mm long, fusiform, stipitate, ciliate and ascending pubescent, the pappus of 2 short awns; disc florets 6–7 mm long, the corolla broadly tubular, the tube short, pilose, the limb basally pilose, the lobes deltoid, anthers dark with dark appendages, ca. 2 mm long, the style branches puberulent, truncate with a short but evident caudate appendix, the style base narrowed into the minute nectary, the ovary laterally compressed, ciliate, with two short awns. *Achene* not seen.

This species differs from *Verbesina sublobata* in having smooth, not scabrous leaves. The leaf bases are gradually acuminate merging into a distinct petiole whereas those of *V. sublobata* are variously truncate or acuminate into a petiole which is cuneiform-winged to the base. *Verbesina lanata* is distinct from *V. oerstediana* with which it may easily be confused, in its pubescent disc corollas, in its larger heads, and in the appearance of the leaves which usually are dry dusty-looking.

PANAMÁ: Roadside below Cerro Campana, *Croat 14233* (MO). Cerro Campana, *Duke 5981* (MO). W slope of Cerro Campana, 2500 ft, *Tyson et al. 2335* (US).

5. **Verbesina oerstediana** Benth. in Örst., Vidensk. Meddel. Dansk Naturhist. Foren. Kjøbenhavn 1851: 96. 1852. TYPE: Costa Rica, *Oersted 94* (K, photo US).—FIG. 74.

Shrub or *tree* to 12 m tall; twigs stout, strongly ridged, becoming terete or merely striate, tomentose with several-celled, weak, mostly collapsing, whitish or brownish hairs, sometimes glandular; axillary buds tomentose. *Leaves* alternate, lanceolate or elliptical, 15–20 cm long, acuminate at both ends, entire or serrulate, lateral veins 5–6 on each side of the midvein, undersides drying lighter, reticulate, above softly and sparingly pubescent with short, weak, often wide-based hairs,

beneath tomentulose with longer hairs which lack broad bases; petiole 1.5–2.5 cm long, slender, pubescent. *Inflorescence* a many-headed, cymose panicle; peduncles slender, pubescent, striate, the ultimate divisions 10–15 mm long; minute bracteoles sometimes subtending the head and appearing as involucral bracts. *Heads* radiate, small, 5–7 mm tall; involucral bracts appressed, acute, in about 2 series, the innermost ca. 2 mm long, dorsally pubescent; paleas about twice as long as the involucral bracts, resembling them and enfolding the florets, persistent after the achenes fall; ray florets few, the corolla yellow, the limb broad, denticulate, ca. 5 mm long, glabrous or pubescent on the ribs beneath, the tube slender, pilose, ca. 2 mm long, the ovary linear-fusiform, glabrate; disc flowers 5–6 mm long, glabrous, the tube short, not well demarcated, the anthers dark with dark appendages, the auricles crumpled, the style branches obtuse, thickened, dorsally pilose, the style base not expanded, the nectary cylindrical, smaller in diameter than the style, the ovary fusiform, laterally flattened. *Achene* body black, linear-fusiform, compressed, 3.5 mm long, prominently winged; pappus of 2 subequal, slender awns ca. 2 mm long.

This species may be recognized by its entire or minutely denticulate leaves and the many-headed panicles of small, radiate, yellow heads. Similar to *V. lanata*, the heads are smaller with smaller involucral bracts, and the leaves appear less pubescent. In fruiting collections, the numerous awns of the achenes are evident emerging from the paleas.

CHIRIQUÍ: Robalo Trail, N slopes of Cerro Horqueta, 6000–7000 ft, *Allen 4966* (MO). "Monte Rey," above Boquete, *Croat 15721* (MO). Palo Alto, 5000 ft, *Stern et al. 1050* (MO). Valley of upper Río Chiriquí Viejo, *White & White 91* (MO).

6. **Verbesina sublobata** Benth., Pl. Hartw. 76. 1841. TYPE: Guatemala, *Hartweg 536* (K, not seen, US, fragment).

Shrub to 3 m tall; stems stout, strongly angled but soon terete and striate, pubescent with weak small hairs, sometimes purplish on one side, in age glabrescent and grey. *Leaves* alternate, ovate to spatulate, apically acute, sometimes 3–5-lobed, basally rounded or acuminate into the winged petiole, the margin minutely callose-dentate, above scabrous and punctate, beneath softly pubescent, the venation elevated; petiole 3–4 cm long, cuneiform-winged to the base, sometimes minutely expanded into auricles. *Inflorescence* a somewhat compacted panicle, the inflorescence branches strongly angled, becoming stout, pubescent, and with minute, obtuse or rounded bracteoles sometimes present. *Heads* to 6–9 mm long, radiate, globose; involucral bracts in 2–3 imbricate series, rounded or obtuse, ciliate, but otherwise glabrate, the innermost largest, ca. 5 mm long; ray florets ca. 6, 10–11 mm long, the corolla white, the limb ca. 6 mm long, narrow, entire or denticulate, glabrous, the tube ca. 2 mm long, puberulent, the ovary compressed, fusiform without a conspicuous stipe, the pappus of two short awns; disc florets numerous, ca. 6 mm long, the corolla pilose on the basal ⅓, glabrous above, the lobes 1–2 mm deep, obtuse, the anthers 2 mm long, dark with light appendages, basally truncate, the style branches narrow with apical appendages, the style base not expanded, smaller than the cylindrical, apically sinuate nectary,

FIGURE 74. *Verbesina oerstediana* Benth.—A. Flowering branch (× 3/5).—B. Achene (× 6 3/10). [After *Croat 15721* (MO).]

the ovary much compressed, ciliate, somewhat oblique. *Achene* body black, whitish tubercular, 3 mm long, broadly winged; pappus of 2 awns ca. 1 mm long.

This species is known in Panama from only one collection which has heads somewhat larger than those of the type collection. Some material from other countries going under this name may be different. The leaf uppersides of *V. sublobata* are quite scabrous. In this species, leaves may be lobed or not.

HERRERA: Road between Las Minas and Pesé, *Duke 12300* (MO).

7. **Verbesina turbacensis** H.B.K., Nov. Gen. Sp. Pl. 4: 203. 1820. TYPE: Colombia, *Bonpland 1456* (P, photo, MO).

Shrub or *tree* to 4 m tall; stems tomentose, with thin petiolar wings. *Leaves* alternate, to 25 cm long, the larger ones sinuate-lobed, minutely callose-denticulate, the midvein prominent, elevated beneath, the minor venation sometimes appearing reticulate beneath, above scabridulous with short, stout-based hairs, beneath softly tomentose with short, verrucose hairs; petiole cuneiform-winged to near the base, mostly distinct from the blade, concaulescent and forming thin wings on the stem in the region of the inflorescence. *Inflorescence* a large, open, many-headed panicle, somewhat flattened; branches stout, tomentulose with short whitish or yellowish-brown hairs; foliose bracts present, scalelike bracteoles sometimes present on the ultimate peduncles, sometimes subtending the head and appearing as part of the involucre, the basal portion of the leaves sometimes concaulescent and forming pairs of green lines between the nodes. *Heads* small, ca. 5 mm high, ca. 4 mm across, radiate; involucral bracts in several unequal series, imbricate, appressed, acute, dorsally pubescent; paleas scarious, folded over the florets, the keel ciliate; ray florets about 8, white, the ligule elliptical, entire, 2–3 mm long, the tube pilose, ca. 1.5 mm long, the ovary lenticular, laterally compressed, ciliate and pubescent on one side, pappus of two small, strigose awns, the dorsal awn the largest; disc florets several, 4–5 mm long, the corolla tubiform, the lower portion pilose, the lobes ventrally papillose, the anthers dark, apically light-appendaged, basally truncate, the style branches truncate, penicillate with a short appendage, the stigmatic lines well marked, the style base expanded-globose, situated against the stout, cylindrical nectary, the ovary laterally compressed-lenticular, sparingly pubescent except apically, the shoulders with 1 or 2 stout, short awns. *Achene* body black, 2.5 mm long, 4-angled, slightly compressed, those of the margins with large, white, tubercular-based trichomes, those of the disc mostly smooth, the wings ca. 1–4 mm wide, white, minutely striate; pappus of two unequal, strigose, short awns.

This species closely resembles *Verbesina gigantea* but the stems are more pubescent and the bracteoles are narrower. The wings on the stems, which are formed by concaulescence of the stem and petioles, are often narrow and sometimes difficult to see.

CHIRIQUÍ: Quebrada de Vuelta, 30 km N of Paso Canoas, 600 m, *Busey 626* (MO). Lava fields near town of Volcán, 4600 ft, *Duke 9217* (MO). PANAMÁ: Cerro Azul, *Croat 13022* (MO). E slope of Cerro Jefe, 2700 ft, *Tyson 3412* (MO).

73. VIGUIERA

Viguiera H.B.K., Nov. Gen. Sp. Pl. 4: 224, *tab.* 379. 1820. TYPE: *V. helianthoides* H.B.K. = *V. dentata* (Cav.) Spreng.

Hymenostephium Benth. in Benth. & Hook.f., Gen. Pl. 2: 382. 1873. TYPE: *H. mexicanum* Benth.

Herbs or *shrubs*; stems and branches mostly slender, puberulent or rarely incanous-tomentose. *Leaves* opposite, often alternate near the inflorescence, mostly entire or serrate, rarely lobed, chartaceous, occasionally coriaceous or textilous; petioles mostly slender, rarely wanting. *Inflorescence* a solitary head or paniculate aggregation of heads; bracts foliaceous; bractlets often wanting. *Heads* mostly radiate, yellow (Panama); involucral bracts in 2–3 series, often dark, slender or broad, mostly alike but often unequal, pubescent; paleas indurate, striate, equalling or exceeding the involucral bracts, the basal, scarious portion completely enfolding the achene; ray florets with a flat pubescent tube, the limb broad or narrow, denticulate or entire, dorsally pubescent, the androecium wanting, the ovary sterile, flat or trigonous, often elongate; disc florets numerous, the tube short, the limb sometimes oblique, pubescent, the 5 lobes dorsally pubescent, the anthers dark, the apical appendages often dorsally glandular, the basal auricles short, the style branches flattened, pilose, with a pilose apicule, the base mostly expanded-globose, stipitate, the ovary somewhat laterally compressed, mostly pubescent. *Achene* compressed-lenticular, sometimes quadrate, unmargined except sometimes at the base, appressed pubescent or glabrous; pappus usually of 2–3 basally broadened awns and intermediate squamellae, the awns or squamellae or both sometimes wanting.

Viguiera may be recognized by its lenticular seeds and uniform, narrowly acute involucral bracts. The pappus may be wanting or may consist of scales or awns or both. The genus is similar to *Simsia* which has flatter achenes and usually more persistent awns. Suggestions that *Viguiera* is confused with *Helianthus*, a genus not occurring in Panama, cannot be maintained. In addition to a number of features noted by other writers, species of *Helianthus* have a conspicuous annular bulge or corolla bulb (Anderson, 1952) near the base of the disc corolla limb.

In Panamanian species of *Viguiera*, the involucral bracts are in two series, the outermost shorter and more pubescent than the inner series which are slightly erose near the apex. The lobes of the disc corollas are noticeably pubescent outside.

Earlier writers who reported *Gymnolomia rudbeckioides* H.B.K. (1820) from Panama were probably referring to *Viguiera cordata*. *Index Kewensis* placed some of the synonyms noted here for *Viguiera cordata* under *Gymnolomia rudbeckioides*. Although they had not seen its type collection, both Robinson & Greenman (1899) and Blake (1918) in their revisions of *Gymnolomia* and *Viguiera* distinguished *Gymnolomia rudbeckioides* from plants of Central America. *Gymnolomia*, here lectotypified by *G. rudbeckioides*, may be the correct name for much

of the New World material which has been placed in the genus *Aspilia* Thouars. *Aspilia* is based on a strand plant of eastern Madagascar.

Literature:

Anderson, E. 1952. Details of the flowers of a sunflower. Missouri Bot. Gard. Bull. 40(7): frontispiece.

Blake, S. F. 1918. A revision of the genus *Viguiera*. Contr. Gray Herb. 54: 1–205.

Robinson, B. L. & J. M. Greenman. 1899. Revision of the genus *Gymnolomia*. Proc. Boston Soc. Nat. Hist. 29: 87–108.

a. Leaves sessile; ray corollas less than 10 mm long; pappus of awns and squamellae ..... 3. *V. tenuis*

aa. Leaves petiolate; ray corollas more than 10 mm long; pappus of awns, squamellae, or wanting.

b. Leaves eglandular beneath; involucral bracts less than 1.5 mm wide; pappus, if present, without awns ..... 1. *V. cordata*

bb. Leaves copiously glandular beneath; some involucral bracts exceeding 2 mm wide; pappus of fimbriate squamellae and 2 basally flattened awns ..... 2. *V. sylvatica*

1. **Viguiera cordata** (Hook. & Arn.) D'Arcy, Phytologia 30: 6. 1975.—Fig. 75.

Gymnolomia microcephala Less., Linnaea 5: 153. 1830. TYPE: not seen, not *Viguiera microcephala* Greenman, Proc. Amer. Acad. Arts 39: 105. 1903.

Wedelia cordata Hook. & Arn., Bot. Beech. Voy. 435. 1841. TYPE: Nicaragua, *Sinclair* (K, not seen).

Gymnopsis costaricensis Benth. in Örst., Vidensk. Meddel. Dansk. Naturhist. Foren. Kjøbenhavn. 1851: 90. 1852. TYPE: not seen.

G. vulcanica Steetz in Seem., Bot. Voy. Herald 157. 1854. TYPE: Panama, Chiriquí Volcano, *Seemann* (not seen).

Montanoa thomasii Klatt, Abh. Naturf. Ges. Halle 15: 328. 1882. TYPE: Mexico, *Thomas* (GH).

Aspilia costaricensis (Benth.) Klatt, Bull. Soc. Roy. Bot. Belgique 31: 201. 1892.

Hymenostephium cordatum (Hook. & Arn.) Blake, Jour. Bot. 53. 268. 1915.

H. microcephalum (Less.) Blake, Contr. Gray Herb. 54: 8. 1918, not *Viguiera microcephala* Greenman, Proc. Amer. Acad. Arts 39: 109. 1903.

Sprawling or erect *herb* to 3 m tall; stems elongate, sometimes purplish, puberulent with weak, whitish, spreading hairs, glabrescent. *Leaves* mostly opposite or nearly so, to ca. 8 cm long, ovate, sometimes broadly so, apically acute or acuminate, basally cordate, rounded or truncate, the margins serrate or dentate, the teeth obtuse, callose-mucronulate, 3-veined from near the base, each pinnately veined, elevated and prominent beneath, puberulent or scabrous with slender, verrucose hairs above, some with stout bases, and on the veins with weak, collapsing verrucose hairs, beneath glabrate to tomentose, sometimes scabridulous with mostly verrucose hairs; petiole slender, to 15 mm long, pubescent, slightly enlarged and indurate at the base. *Inflorescence* a loose, terminal aggregate of several heads; peduncles short or to 30 cm long, pubescent; bracts foliaceous, solitary bracteoles sometimes present. *Heads* radiate, mostly 20–25 cm across and 8 mm tall; involucral bracts numerous in ca. 2 similar, unequal series, lanceolate or ovate, subherbaceous, apically acute, strongly 7–5-nerved, ascending-strigose, 4–6 mm long, callose or minutely erose at the tip; paleas resembling the inner involucral bracts, but longer, indurate, striate, ca. 6 mm long, enfolding the ovary, ciliate on the keel; ray florets 6–10, the corolla yellow, the tube 1–1.5 mm

FIGURE 75. *Viguiera cordata* (Hook. & Arn.) D'Arcy.—A. Flowering branch (× ½).—B. Achene (× 30). [After *Tyson et al.* 2829 (MO).]—C. Achene (× 15).—D. Base of style and nectary (× 14⅖). [After *Croat* 9659 (MO).]—E. Base of style and nectary (× 14⅖). [After *Croat* 13628 (MO).]

long, pilose, the limb elliptical, ca. 13 mm long, entire or denticulate, with a few strigose hairs near the base, the ovary sterile, compressed, pubescent, epappose; disc florets numerous, ca. 5 mm long, the corolla ca. 4 mm long, the tube pilose, the limb slightly broadening upwards, apically strigose and the lobes dorsally strigose, the anthers dark, 2–3 mm long, dorsally glandular, the style base expanded or not, the nectary cylindrical, the ovary compressed, glabrous or pilose, the pappus of small scales or wanting. *Achene* black, ca. 2 mm long, compressed, minutely striate, glabrous or pilose with long, ascending hairs near the base; pappus wanting or of 1–3 small, hyaline, fimbriate scales.

This species displays puzzling variation in characters of the style base and achene, and two distinctive forms appear in Panama. Either the style base is conspicuously enlarged above the nectary and the achene is copiously pilose and eppapose, or the style base is not at all expanded and the achene is glabrous with a distinct squamellate pappus. Blake (1918) devoted considerable attention to these differences but decided they were of little taxonomic value. The type collection of *Montanoa thomasii* is intermediate: the style base is hardly expanded, and the achene is glabrate with very few long hairs, lacking a pappus. In Panamanian material, the difference noted could not be correlated with any other differences in the plants. Although a type specimen was not seen, the material included here matches a range of specimens annotated as *Hymenostephium cordatum* by S. F. Blake.

Viguiera cordata may be recognized by its yellow, radiate heads and the usually grey-pubescent involucral bracts which contrast with the longer, blackish, striate paleas. It is known mainly from lower and middle elevations. The species ranges widely in tropical America.

CHIRIQUÍ: Trail from Paso Ancho to Monte Lirio, upper valley of the Río Chiriquí Viejo, 1500–2000 m, *Allen 1585* (MO, NY, US). Forested hill N of Audubon Cabin Bambito, *Croat 13628* (MO). Nueva Suisa, Volcán District, 6000 ft, *D'Arcy 5324* (MO). Near Boquete, 3300–4200 ft, *Lewis et al. 574* (MO). Pastures around Boquete, 1000–1300 m, *Pittier 2904* (US). COCLÉ: Trails near Finca Tomas Arias, El Valle de Antón, 600 m, *Allen 4227* (MO). Near El Valle de Antón, *Croat 13278* (MO). Penonomé and vic., 50–1000 ft, *Williams 145* (NY). HERRERA: Roadside between El Potrero and Las Minas, *Croat 9659, 9661* (both MO). 10 mi S of Ocú, *Tyson et al. 2813, 2829* (both MO).

2. **Viguiera sylvatica** Klatt, Bull. Soc. Roy. Bot. Belgique 31: 204. 1892. TYPE: Costa Rica, *Pittier 779* (GH, not seen).

Erect *herb* to 3 m tall; branches slender, finely striate, sparingly pilose with long white hairs, glabrescent. *Leaves* alternate, (?opposite below), mostly ovate and to 12 cm long but sometimes broadly ovate and 20 cm long, apically acuminate, basally obtuse or short acuminate, the margins serrate, 3-nerved from just above the base, chartaceous, sparingly pubescent, glandular beneath, sometimes scabridulous above and drying darker; petioles slender, mostly 5–12 mm long, sometimes pilose, but on large leaves longer, stouter and glabrescent. *Inflorescence* mostly an open, ill-defined panicle but sometimes somewhat compact and cymose; peduncles somewhat stout, to ca. 4 cm long, the appressed tomentum obscuring the glandular, often strongly striate surface, subtended by linear bracts. *Heads* globose, 10–13 mm tall, radiate, but the rays sometimes few and inconspicuous;

involucral bracts in 2 similar and subequal series, ca. 8 mm long, lanceolate, indurate and striate, sparingly pubescent, drying glandular; paleas oblong, indurate, striate, the costa dark, apically excurrent and acute, equalling or slightly exceeding the involucral bracts, the margin scarious, dorsally puberulent, the basally scarious, corrugated portion completely enveloping the floret; ray florets 6–8, the corolla apparently fugaceous, ca. 15 mm long, the tube ca. 1 mm long, flattened, pilose, the limb elliptical, yellow, apically entire or notched, dorsally pubescent, the ovary sterile, elongate, trigonous or flat, 3–4 mm long, dorsally pubescent; disc florets numerous, 8–10 mm long, the corolla 4–5 mm long, the tube short, the limb basally oblique, puberulent, the lobes dorsally pilose, the anthers black, ca. 3 mm long, the appendages narrow, dorsally glandular, the basal auricles short, the style branches flattened, dorsally pilose, truncate with a conspicuous acicular, pilose apicule, the style base expanded, cylindrical-globose, stipitate above an elongate, cylindrical nectary. *Achene* black, ca. 4 mm long, only slightly compressed, ascending-pilose; carpopodium conspicuous, slightly swollen; pappus of two basally hyaline-squamellous, stiff, strigulose awns, and a slightly interrupted hyaline ring of erose scales dorsal to the awns, the nectary remaining as an apical peg.

This species is known in Panama from only one collection taken in January 1939. It ranges into Costa Rica where it occurs at middle or upper elevations.

Similar to *Viguiera cordata*, this species is distinguished by the looser involucre, the paleas which are black along the costa to the pointed tip instead of only below the tip, and the two awns which accompany the ring of scales to make up the pappus. The carpopodium is also larger.

Because of the paucity of Panamanian material, part of the above description is taken from *Worthen*, Costa Rica (MO).

CHIRIQUÍ: Trail from Paso Ancho to Monte Lirio, upper valley of the Río Chiriquí Viejo, 1500–2000 m, *Allen 1495* (MO, NY).

3. **Viguiera tenuis** A. Gray in Wats., Proc. Amer. Acad. Arts 22: 426. 1886. TYPE: Mexico, *Palmer 657* (MO, NY).

Wiry *herbs* to 50 cm tall; stems slender, pubescent with appressed, ascending, white, verrucose hairs, more conspicuous below; roots short and fibrous. *Leaves* opposite, narrowly oblong or lanceolate, to 4 cm long, rarely ovate, inconspicuously denticulate, obscurely 3-veined from near the base, both sides appressed-canescent; petiole short or wanting. *Inflorescence* an open, several-headed terminal panicle; peduncles becoming narrower upwards, expanding slightly and whitish-pubescent at the apex; bracts subtending the branches and alternate along the branches, foliaceous but smaller and narrower upwards. *Heads* radiate, globose, to 10 mm across; involucral bracts narrow, imbricate in several series of equal length, the outermost linear, the inner series broader, all appressed-canescent and whitish except for the dark green tips; paleas exceeding the involucral bracts; ray florets several, 8 mm long, the corolla yellow, 4 mm long, the limb ca. 3 mm wide, emarginate, glabrous, the tube short, pubescent, the ovary linear, sterile, ca. 4 mm long, ascending pubescent, the pappus wanting; disc florets numerous,

ca. 5 mm long, the corolla broadly tubular, ascending-pilose, the lobes ventrally papillose, dorsally hispid, the tube short, sharply contracted, the anthers ca. 1.5 mm long, basally sagittate, the light-colored appendages with a darker costa, the filaments glabrous, the anther column conspicuous, the style branches slender, dorsally long-pilose, the style base expanded, stipitate above a short nectary, the ovary compressed-lenticular, ca. 2 mm long, densely ascending-pilose, the pappus of two awns and 4 broad, hyaline, fimbriate scales. *Achene* body 2 mm long, dark but covered with long, ascending-hispid, stramineous hairs; pappus of 4 large, rotund, apically erose scales and two basally flattened, strigose awns ca. 5 mm long.

COCLÉ: Near Olá, 100–130 m, *Pittier 5033* (US).

74. WEDELIA

Wedelia Jacq., Enum. Pl. Carib. 8, 28. 1760; Sel. Stirp. Amer. 217. 1763. TYPE: *W. fruticosa* Jacq.

Herbs or *shrubs*, erect, ascending or sometimes procumbent; stems slender or stout and succulent; rootstock stout or fibrous. *Leaves* opposite, the margins lobed or not, mostly dentate or serrate and scabrous, the indumentum of glandular trichomes and of verrucose hairs; petioles elongate, short or wanting, united to form a distinct intrapetiolar ridge. *Inflorescence* of 1–several long-pedunculate, ebracteate heads at a node. *Heads* radiate, globose, campanulate or funnelform; involucral bracts several in 2–4 dissimilar series, the outermost narrower, often basally indurate and stramineous and apically green, mostly scabrous on both sides, the innermost often entirely stramineous, rounded or obtuse, ciliate and sometimes pubescent dorsally; receptacle flat or slightly convex; paleas hyaline, somewhat indurated, enfolding the florets, the erose or ciliate, deltoid apex often folded over the floret in bud, the costa prominent, occasionally excurrent; ray florets several, the corollas yellow or white, broad, 2–3-denticulate, the anthers wanting, the style branches slender, elongate and outcurving, the base not expanded but immersed in the tall, cylindrical nectary, the ovary compressed, sometimes angled or winged, glabrous or pubescent, apically contracted below the coroniform, scaly pappus, the awns mostly wanting or one or more of the erose scale elements produced into small awns; disc florets mostly numerous, tubular, the 5 deltoid lobes pubescent inside and out, the tube often pubescent on the veins and just above the base, the 5 anthers black with deltoid, black, yellow or transparent appendages and short or long, connate basal auricles, the style branches somewhat flattened, pilose, apically acicular, the style base not enlarged, immersed in the tall, cylindrical nectary, the ovary angled, slightly compressed, apically contracted below the pappus, the pappus resembling that of the rays. *Achenes* often unlike in the same head, sometimes clearly dimorphic, differing in shape, size, color, pubescence and texture, the outermost often flattened, the margins sometimes with massively thickened wings, the innermost clavate, 3–4-angled but the angles not thickened, all apically contracted and surmounted by a coroniform pappus of fused, erose or ciliate scales, sometimes produced into one or two short awns.

A genus of over a dozen species mainly of the Caribbean area, *Wedelia* may be recognized by the salient green involucral bracts or their apices, or by the contracted achene apices surmounted by a small, peglike, coroniform pappus of minute, fused scales. Several sections have been recognized in *Wedelia* and two distinct elements are present in Panama. *Wedelia trilobata* is related to species in the Antilles and South America, and some Panamanian collections are suggestive of these species. The group has succulent leaves, more or less homogeneous green involucral bracts and glandular achenes. The balance of the Panamanian *Wedelia* species are more or less erect plants with thin, scabrous leaves, graded involucral bracts, and sometimes pubescent but not glandular achenes. *Wedelia fruticosa* Jacq. of northern South America has been reported from Panama but the cited specimens when examined turned out to be other species. *Wedelia fruticosa* has small, mostly rounded leaves, broad involucral bracts, and eglandular stems and leaves.

Several Panamanian collections from upland Chiriquí may represent a species distinct from those treated here. Much like plants of *W. calycina*, these collections have much smaller flowers and leaves which are smaller, narrower, and tend to have shallow, irregular lobing in the basal half.

Material now available is not adequate for determination or construction of a good species description.

CHIRIQUÍ: Near El Hato del Volcán, *Croat 10712* (MO). Volcán on grounds of Escuela San Benito, *Croat 10412* (MO). Above Boquete on road past Princesa Janca coffe finca, *D'Arcy & D'Arcy 6338* (MO). Above Boquete on slope of La Popa, 5400 ft, *D'Arcy & D'Arcy 6392* (MO). Llanos del Volcán, 1120–1200 m, *Seibert 338* (MO).

Literature:

Schultz, O. E. 1911. *Wedelia. In* I. Urban, Symb. Antil. 7: 94–115.

a. Leaf base extended into an abruptly terminating petiolar wing; leaves often 3-lobed, glandular beneath; plants procumbent; ray corollas glandular outside; achenes glandular, not pubescent ---------- 5. *W. trilobata*
aa. Leaf base narrowed into the petiole; leaves seldom 3-lobed, eglandular; plants erect; corollas eglandular; achenes glabrous or pubescent, eglandular.
  b. Involucre pilose; achenes thin-winged; petiole margins long-pilose ---------- 3. *W. keatingii*
  bb. Involucre pubescent but not pilose; achenes unwinged or thick-winged; petiole margins not long-pilose.
    c. Some involucral bracts more than 5 mm wide; achenes distinctly dimorphic, some compressed with massively thickened margins, others 3–4-angled without thickened margins, more than 5 mm long; some leaves more than 30 mm wide ---------- 1. *W. calycina*
    cc. Involucral bracts less than 5 mm wide; achenes often dissimilar but not of two distinct classes, mostly 3–4-angled, less than 5 mm long; leaves mostly less than 30 mm wide.
      d. Leaves mostly obtuse apically, scabrous but lacking a pubescence of minute hairs; upland plants ---------- 4. *W. parviceps*
      dd. Leaves mostly acute or acuminate apically, scabrous and densely pubescent with minute hairs; lowland plants ---------- 2. *W. inconstans*

1. **Wedelia calycina** L. C. Rich. in Pers., Syn. Pl. 2: 490. 1807. TYPE: Guadeloupe, *Richard* (?P, not seen).

W. acapulcensis H.B.K., Nov. Gen. Sp. Pl. 4: 215. 1819. TYPE: Mexico, *Bonpland* (P).
W. caracasana DC., Prodr. 5: 541. 1836. TYPE: Venezuela, *Vargas* (G-DC, not seen, photo MO).

W. acuminata DC., Prodr. 5: 541. 1836. TYPE: Cuba, *Ossa* (not seen).
W. scaberrima Benth., Ann. Nat. Hist. 2: 110. 1839. TYPE: Guyana, *Schomburgk 128* (BM, holotype, not seen; G, isotype, not seen, MO, photo).
W. hookeriana Gard., London Jour. Bot. 7: 289. 1848. TYPE: Brasil, *Gardner 2219*.
W. villosa Gard., London Jour. Bot. 7: 289. 1848. SYNTYPE: Brazil, *Gardner 1349* (W, not seen, MO, photo); *1730* (BM).
W. jacquini E. O. Schulz in Urb., Symb. Ant. 7. 100. 1911, not L. C. Rich. in Pers. 1807, nom. illeg. based on *W. fruticosa* Jacq.

Erect or scrambling *shrub* to 3 m tall; stems slender, spreading-pubescent, glabrescent, minutely glandular, drying finely angled. *Leaves* ovate, apically acuminate, basally rounded or short acuminate, the margins serrate, the veins prominent beneath, obscure above, 3-nerved from somewhat above the base, drying darker above, both sides scabrous with erect and ascending stout hairs, the minor venation glandular beneath; petioles slender, ca. 1 mm long, united in an intrapetiolar ridge. *Inflorescence* of 1–several heads at a node; peduncles slender, pubescent, to 5 cm long. *Heads* radiate, campanulate to globose; involucral bracts several in about 2 dissimilar series, the outermost ca. 15 mm long, basally distinct, lanceolate, indurate and stramineous below, the upper green portion scabrid on both sides, the innermost bracts indurate, stramineous, obtuse or rounded, ciliate and sometimes dorsally pubescent; paleas ca. 7 mm long, hyaline, grading narrower inwards, the innermost oblong, contracted below the ovate, erose apex, the costa prominent; ray florets showy, 15–20 mm long, the corolla yellow, sometimes drying white, 2-dentate, glabrous, the style branches sometimes green, the ovary fertile, pilose, slightly trigonous; disc florets numerous, ca. 8 mm long, the 5 lobes dorsally and ventrally puberulent, the stamens black with narrowly deltoid, yellow appendages and elongate basal auricles, the style branches slightly flattened, pilose, the style base not expanded, immersed in the cylindrical ovarial disc, the ovary pubescent, angled, mostly awnless. *Achenes* 5–6 mm long, dimorphic in shape and color, puberulent, clavate, strongly angled and slightly compressed, or glabrous and flattened, with massively thickened, winglike angles.

This species is here interpreted broadly to include both Antillean and mainland American plants, and may include a number of infraspecific taxa. Schulz (1911) considered most mainland plants to have more deeply lobed ligules and be specifically distinct from plants of the Antilles. *Wedelia aequatoreale* Spruce has slightly larger and heavier involucral bracts than most Panamanian plants, but a few collections are quite similar to the Spruce material.

Fruits of this species display heterocarpy: the ray achenes are compressed and curved with thick wings or margins while the disc achenes are little compressed, 3–4-angled, clavate, slightly smaller, and usually pubescent with a different color. The plump wings or margins are unlike the thin wings in the related genus *Verbesina* and in *Wedelia keatingii*.

In Panama, *Wedelia calycina* is restricted to the lowlands, and most collections are from areas of disturbance and secondary growth. It is sometimes reported to be a climber.

CANAL ZONE: Near Paraíso, *Croat 7159* (MO). Hill S of Pedro Miguel Locks, *Croat 9174* (MO). Road C2C on Cerro Luisa, *Croat 10771* (MO). NW of Pedro Miguel, *Croat*

12261 (MO). Farfan Beach, *D'Arcy & D'Arcy 6074* (MO). Fort Kobbe, *Duke 4211* (GH, MO). Military Road K-9, *Ebinger 517* (MO). Chagres, *Fendler 167* (GH, MO). Ancón Hill, *Killip 12053* (GH). 2 mi W of Ferry Thatcher Bridge, *Lazor 2197* (MO). 5 mi N of junction Interam. Hwy. and C-10 Artillery road, *Lazor 5455* (MO). Farfan Beach area, *Lazor & Tyson 5718* (MO). Chiva Chiva Trail, ½ mi above Red Tank, *Maxim & Harvey 6593* (GH). Ancón Hill, *Maxim 6777* (GH). Curundú, *McDaniel 5184* (MO). Between Rodman Marine Base and Chorrera, *Nowicke et al. 3599* (MO). Ancón Hill, *Piper 5580* (GH). Between Corozal and Ancón, *Pittier 2642* (GH). W slope of Ancón Hill near Balboa, *Seibert 386* (GH, MO). Ancón Hill, *Standley 25187* (GH). Corozal Road near Panamá, *Standley 26866* (GH). Near Río Cocoli, Road K-9, *Stern et al. 16, 329* (both GH, MO). Chiva Chiva Trail near Miraflores Lake, *Tyson 1409* (MO). Farfan Beach area, *Tyson 1818* (MO). Fort Amador, *Tyson 2029* (MO). Farfan Beach area, *Tyson & Blum 2622, 2624* (both MO); *Tyson et al. 3173* (MO). Fort Clayton, *Tyson & Blum 3896* (MO). Near Miraflores, *White & White 51* (MO). W slope of Ancón Hill, *Woodson et al. 1319* (GH, MO). COCLÉ: Hills S of El Valle de Antón, 6–800 m, *Allen 2858* (MO). 3 mi NE of Antón, *Croat 9614* (MO). Penonomé, *Dwyer 2004* (GH, MO). 12 mi NE of Penonomé, 1200 ft, *Lewis et al. 1515* (GH, MO). COLÓN: Under Colón Highway bridge on Chagres River, *Lazor & Tyson 3043* (MO). HERRERA: Ocú, *Ebinger 1044* (MO). PANAMÁ: Río Charco-Espiritu on Tocumen Highway, *Duke 5698* (GH, MO). Tumba Muerto, *Heriberto s.n.* (GH). Taboga Island, *Macbride 2793* (GH). Around Alhajuela, Chagres Valley, *Pittier 2331* (GH), *3451* (GH, MO). Sabana de Juan Corso near Chepo, *Pittier 4521* (GH). Near Arraiján, *Woodson et al. 1371* (GH, MO). Isla Taboga, *Woodson et al. 1469* (GH, MO). Ca. 5 mi NE of La Mesa, *Blum & Tyson 672* (MO).

2. **Wedelia inconstans** D'Arcy, Phytologia 30: 5. 1975. TYPE: Panama, *Croat 15241* (MO).

Erect *herb* or *subshrub* to 1 m tall; stems slender, copiously pubescent with spreading hairs and glandular trichomes, glabrescent. *Leaves* opposite, deciduous from lower parts of the stem, to 6 cm long and 2.5 cm wide, ovate, apically obtuse to acuminate, basally rounded, obtuse or acuminate, the margins inconspicuously serrate, the venation often obscure, both sides softly tomentose to scabrous with ascending whitish hairs, glandular on the minor venation beneath; petioles short, to 4 mm long, scabrous. *Inflorescence* of 1–2 heads at a node; pedicels slender, to ca. 4 cm long, hispid. *Heads* radiate; involucral bracts several in 2–3 series, the outermost narrowly ovate, apically acuminate, basally indurate, green above and pubescent on both sides, 8–9 mm long, the inner series mostly indurated and stramineous, obtuse or rounded, ciliate, often dorsally pubescent; receptacle somewhat convex; paleas hyaline, oblong, 4–7 mm long, constricted below the ovate, erose apex, the costa prominent; ray florets several, to 10 mm long, the corollas yellow (?or white), 8 mm long, exserted ca. 5 mm, 2-denticulate, puberulent along the main angles and low on the tube, the style branches yellowish, the ovary flattened, pubescent or glabrous; disc florets several, ca. 6 mm long, the 5 corolla lobes pubescent inside and out, the tube puberulent, the anthers black with narrowly deltoid yellowish appendages, the basal auricles short, the style branches somewhat flattened, dorsally pubescent, apically acicular, the base not expanded, the nectary narrowly cyathiform, 0.5 mm high, the ovary compressed, sometimes pubescent, the pappus with one or more scales produced into short, smooth awns. *Achenes* variable within a head, less than 5 mm long, tan, mottled, somewhat pubescent and partially tuberculate, ranging from strongly 3–4-angled and clavate to flattened with heavily thickened margins, apically constricted below the peglike, coroniform pappus of fused scales and sometimes one or more small awns.

This species is similar to *Wedelia calycina* but differs in its smaller, narrower leaves, overall pubescence, and in its smaller heads and achenes. It occurs in sun and shade mainly in disturbed areas of the Pacific coast lowlands. It is similar to *W. parviflora* L. C. Rich of the Antilles, but the type of that species has larger, less pubescent leaves.

COCLÉ: Hills S of El Valle de Antón, 600–800 m, *Allen 2858* (MO). Santa Clara Beach, *Croat 9582* (MO). Ca. 1 mi E of Santa Clara Beach, *D'Arcy & Croat 4086* (MO). El Valle, *Dwyer 1803* (GH, MO, NY). Between Las Margaritas and El Valle, *Woodson et al. 1256* (MO, NY). HERRERA: Road between Las Minas and Pesé, 600 ft, *Duke 12302* (MO). 10 mi S of Ocú, *Tyson et al. 2857, 2858* (both MO). PANAMÁ: Near end of Tocumen Airport runway, *Croat 9769* (MO). Roadside on way to Cerro Campana, *Croat 12022* (MO). Near Madden Lake N of Calzada Larga, *Croat 12926* (MO). Between Chepo and El Llano, *Croat 14492* (MO). Roadside along approach to Cerro Jefe, *Croat 15241* (MO). Ca. 13 mi W of Chepo, *D'Arcy & D'Arcy 6030* (MO). Savanas between Panamá and Chepo, *Dodge et al. 16655* (MO). Near bridge at Nueva Gorgona, *Duke 4540* (MO). Riomar, near Río Mar, *Ebinger 503* (MO). Savanas near Chepo, *Hunter & Allen 36* (MO). Cerro Campana, *Porter et al. 4172, 4320* (both MO). E of Pacora, *Woodson et al. 724* (MO).

3. **Wedelia keatingii** D'Arcy, Phytologia 30: 5. 1975. TYPE: Panama, *Allen 4212* (MO-1600341, holotype; MO, isotype).—FIG. 76.

Herb to 1 m tall; stems weak, branching, puberulent with minute, spreading verrucose hairs and scattered stout, multicellular hairs; roots weakly developed. *Leaves* opposite, ovate, to 10 cm long, apically acuminate, basally obtuse or short acuminate, the margins serrate, the venation appearing pinnate or 3-nerved from near the base, sometimes reticulate beneath, both sides with scattered, stout, white, appressed hairs, scabridulous above; petiole short, sometimes to 3 cm long, winged upwards, the keel strigose. *Inflorescence* undifferentiated, mostly solitary or small clusters of heads on slender peduncles to 2.5 cm long; bractlets wanting. *Heads* radiate, small, to 8 mm long; involucral bracts ca. 10, the outer 4–5 herbaceous, oblong, slightly shorter, apically rounded; paleas scarious, completely enveloping the ray floret, apically erose-obtuse, the costa darkened, prominent; receptacle flat or slightly convex, 2–3 mm across; ray florets about 5, 7–8 mm long, slightly shorter than the outer involucral bracts, the corolla white, ca. 5 mm long, the tube compressed, short, glabrous, the limb broad, flattened-induplicate in bud and short ciliate on the angles, apically 2-notched, the style branches slender, the ovary flattened, the body narrowly oblong-turbinate, ciliate at the angles and puberulent apically, contracted at the apex and expanding into a fimbriate-squamellate pappus, awns wanting; disc florets about 15, ca. 4 mm long, the corolla yellowish, the tube forming almost half the length, the limb cylindrical, the 5 apical lobes dorsally puberulent, the anthers black, 1.5 mm long with transparent, small apical appendages, basally subauriculate, the style branches tomentose, white, with a distinct, subulate apical appendage, the ovary flattened laterally, ciliate, apically contracted and expanded again into the pilose-squamellate pappus which may include one or more short, stout, ascending-strigose awns. *Achenes* black, compressed, with conspicuous wings and sometimes falling with the paleas, the body compressed quadrangular, the lateral (flattened) angles rounded, the sides with elongate, white, ascending, appressed hairs, the wings broad, striate-reticulate,

FIGURE 76. *Wedelia keatingii* D'Arcy.—A. Habit (× 3/5).—B. Central floret (× 6 3/10).—C. Achene with subtending palea (× 10 7/10). [After *Allen 4212* (MO).]

streaked with brown, ?glandular cells; carpopodium a yellowish, smooth area on the lower ventral side flush with the achene body; pappus of a ring or cup of pilose-squamellate processes and sometimes one or two short stout, strigose awns.

This species differs from other species of *Wedelia* in its broadly winged achenes which sometimes have persistent awns and in the narrow, herbaceous outer phyllaries. It would appear to be closely related to *Wedelia calycina* and *W. parviflora* in Panama and to *Calyptocarpus vialis* Less. a species of warm parts of the New World which has not yet been recorded from Panama. It differs from the two species of *Wedelia* just mentioned in its prominently winged achenes which appear to be of one type, while it differs from the *Calyptocarpus* species in its narrow outer involucral bracts. *Calyptocarpus* also has both winged and unwinged achenes in the same head.

COCLÉ: Trails and clearings N of El Valle de Antón, 700–800 m, *Allen 4212* (MO). El Valle, ca. 650 m, *Croat 25280* (MO). Without locality, *Duke 6156* (MO). Hills above El Valle, 1000 m, *Gentry 6902* (MO). Granitic river gorge, 12 NE of Penonomé, 1200 ft, *Lewis et al. 1509* (MO).

4. **Wedelia parviceps** Blake, Contr. U.S. Natl. Herb. 24: 28, *pl.* 9. 1931. Guatemala, *Blake 7681* (US-989584).

Perennial *herb* or *subshrub* to 50 cm tall, usually with several shoots from a woody rootstock; stems slender, scabridulous with ascending and spreading hairs. *Leaves* elliptical to ovate, to 3.5 cm long, 12 cm wide, apically rounded, obtuse or sometimes acute, basally acute or acuminate, the veins prominent beneath, obscure above with 3 main veins from just above the base, the margins inconspicuously serrate, scabrous on both sides with ascending whitish hairs; petioles short, less than 2 mm long, pubescent. *Inflorescences* 1–several heads at a node; peduncles slender, scabrous, mostly drying dark. *Heads* radiate, small, 5–7 mm tall; involucral bracts several in ca. 2 unlike series, the outermost ca. 3 mm long, ovate, indurate and stramineous except for the green tips, the innermost bracts slightly larger with green tips or entirely stramineous; receptacle flat or slightly convex; paleas hyaline, ca. 2 mm long, apically erose or ciliate, sometimes dorsally puberulent, the costa prominent and sometimes apically excurrent; ray florets several, the ligules yellow, ca. 6 mm long, 2-denticulate, puberulent on the principal veins, the ovary fertile, glabrous, the awns wanting; disc florets several, ca. 6 mm long, the corolla lobes puberulent, the tube puberulent near the base, the anthers black with whitish appendages, the basal auricles short, the style branches somewhat flattened, pilose, apically acicular, the style base not expanded, the nectary narrowly cylindrical, 0.6 mm high, the ovary pubescent, flattened. *Achenes* dimorphic, those of the ray florets trigonous, tuberculate, grayish with massively thickened margins, those of the disc florets clavate, black, the margins not thickened and the surface not tuberculate, 3–4 mm long.

This species is distinct among Panamanian *Wedelia* species in its small heads, wiry diminutive aspect, and small leaves. First described from Guatemala, in Panama it is found mainly in upland Chiriquí although one collection, *Dwyer et al. 7564*, was taken in lowland Veraguas Province.

Wedelia parviceps is sometimes confused with *Baltimora recta* L., a lowland species with sterile rays and broader leaves, the three nerves of which arise at the base rather than just above the base as in species of *Wedelia*.

CHIRIQUÍ: 4 mi from Boquete toward Dolega, 4500 ft, *Dwyer & Hayden 7614* (MO). 4.1 mi from Boquete on road to David, *Kirkbride 87* (MO, NY). Alto Boquette, 1125 m, *Partch 69-81* (MO). Around Boquete, 1000 m, *Pittier 2867* (MO). Gualaca in savanas, *Pittier 4346* (GH). Llanos Francia, Boquete District, 3300 ft, *Stern et al. 1185* (GH, MO). VERAGUAS: 2 mi W of Santiago, *Dwyer et al. 7564* (MO).

5. **Wedelia trilobata**[49] (L.) Hitchc., Rep. Missouri Bot. Gard. 4: 99. 1893.

Silphium trilobatum L., Syst. Nat., ed. 10. 2: 1233. 1759. Based on Plumier, Pl. Amer. 97, *tab. 107, fig. 2.* 1755.
Wedelia carnosa L. C. Rich. in Pers., Syn. Pl. 2: 490. 1807. TYPE: Herb Rich (P).

Procumbent perennial *herb*; stems stout, glabrous or pubescent, seldom scabridulous; roots fibrous. *Leaves* opposite, somewhat succulent, to 18 cm long, elliptic or lanceolate, often with 3 angular lobes and conspicuous marginal teeth, apically acute, basally cuneate, glabrous or sparingly pubescent, sometimes scabrous; petiole distinct but less than 5 mm long, the intrapetiolar ridge persistent and conspicuous on old stems. *Inflorescence* of solitary heads on elongate, ebracteate peduncles. *Heads* radiate; involucre green, of several lanceolate, ciliate, obscurely nerved bracts 10–15 mm long, the innermost narrower; paleas hyaline, cuculate, partially enfolding the disc florets, contracted below the deltoid apex; ray florets 4–8, the ligules showy, yellow, 15–20 mm long, broad, glabrous, 3–4-denticulate, the ovary fertile, trigonous; disc florets numerous, ca. 2 cm long, the corolla yellow, 5–6 mm long, the 5 deltoid lobes dorsally glabrous, ventrally pubescent, the tube narrowed below, the anthers black, ca. 3 mm long with blackish appendages and short basal auricles, the style branches flattened and marginally pubescent, the style not basally expanded, the nectary 1 mm high, cylindrical, the ovary 3–4-angled, slender, the pappus lacking awns. *Achenes* blackish, sometimes mottled, clavate, angled, ca. 5 mm long, apically contracted and expanded into a small peglike, coroniform pappus of fused scales.

A native of the New World tropics, this species is widely cultivated as an ornamental ground cover and is now naturalized in many countries. Commonly found along seacoasts, *Wedelia trilobata* also occurs naturally inland in disturbed, wet places. The solitary yellow flowers and thick, mostly 3-lobed leaves on crawling stems are good features for recognition in the field.

Wedelia brasiliensis (Spreng.) Blake (= *W. paludosa* DC.) is closely related but differs from *W. trilobata* in its entire leaves and upright habit. Some Panamanian collections resemble *W. brasiliensis* but cannot be separated specifically from *W. trilobata* growing in the country. Similarly, *W. gracilis* L. C. Rich. of the Greater Antilles has smaller, more saliently lobed and generally pubescent leaves, and the few Panamanian collections resembling *W. gracilis* are better considered as extremes of *W. trilobata* rather than as a separate taxon. "Clavellin de Playa."

BOCAS DEL TORO: Santa Catalina, *Blackwell et al. 2715* (MO). Almirante, *Blum 1320* (MO). Bocas del Toro, *Carleton 134* (GH). RR track near station at mi 5, *Croat & Porter 16487* (MO). Columbus Island, *Dodge 3464* (GH). Chiriquicito to 5 mi S along Río Guarumo, *Lewis et al. 2006* (GH, MO). Isla Colón, *Wedel 73* (GH, MO). Without locality,

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[49] For a list of synonyms see Schulz (1911). Only the listed names are pertinent to Panamanian material.

Wedel 223 (GH, MO). Vic. of Chiriquí Lagoon, *Wedel 1147* (MO), *1792* (GH, MO), *2768* (GH), *2943* (MO). CANAL ZONE: Pipeline Road near Gamboa, *Clewell & Tyson 3274* (MO). Coco Solo road ½ mi from Transisthmian Hwy., *Correa 61* (MO). Barro Colorado Island, *Croat 4264, 6117, 15166* (all MO). Near Coco Solo Weather Station, *Duke 4288* (MO). Just E of Gatún Locks, *Duke 4295* (MO). Toro Point, Fort Sherman, *Duke 4322* (MO). Frijoles, *Ebinger 314* (MO). Chagres, *Fendler 168* (GH, MO). Cristobal, *Greenman & Greenman 5216* (MO). Gatún, *Heriberto 59* (GH). Between Frijoles and Monte Lirio, *Killip 12118* (GH). 1 mi N of JOTC Center at Ft. Sherman, *Lazor 5369* (MO). Cristobal, *Salvoza 1012* (GH). Old Fort San Lorenzo, *Tyson 1554* (MO). Fort Sherman, *Tyson 2255* (MO). COLÓN: Miguel de la Borda, *Croat 9810* (MO). Near Miguel de la Borda, *Croat 9884* (MO). Road to Portobelo ¼ mi N of María Chiquita, *Croat 11350* (MO). Beach strand W of Portobelo, *Croat 14133A* (MO). Santa Rita Ridge, *D'Arcy & D'Arcy 6142* (MO). W of Portobelo, *D'Arcy & D'Arcy 6702* (MO). María Chiquita, *Ebinger 436* (MO). Mouth of Río Piedras, *Lewis et al. 3169* (MO). Colón, *Macbride & Featherstone 9* (GH). Near Santa Isabel, *Pittier 4182* (GH). Around Portobelo, *Pittier 2467* (GH). Beach between Fató and Playa de Damas, *Pittier 3926* (GH). 5 mi NE of Sabanita, *Wilbur & Luteyn 11622* (MO). LOS SANTOS: Río Tonosí near Tonosí, *Lewis et al. 1587* (GH, MO). PANAMÁ: Pedro Gonzalez, Pearl Island, *Allen 2588* (MO). San José Island, *Erlanson 1* (GH); *Johnston 490* (GH); *Harlow 23* (GH). Chimán, *Lewis et al. 3347* (MO). Taboga Island, *Pittier 3612* (GH). Saboga Island, *Tyson & Loftin 5131* (MO). Isla Espiritu Santo, Pearl Islands, *Tyson 5572* (MO). SAN BLAS: Hills SE of Puerto Obaldía, *Croat 16722* (MO). Near Puerto Obaldía, *Croat 16969* (MO). Airport at Irandí, *Duke 6514* (GH, MO). Mulatuppu, *Duke 8524* (MO). Mainland opposite Achituppu, *Lewis et al. 88* (MO). Nargana Island, *Gentry 1513* (MO). W end of Soskatupu, *Kirkbride 207* (MO). VERAGUAS: Mouth of Río Concepción, *Lewis et al. 2827* (MO).

75. WULFFIA

Wulffia Neck. ex Cass. in Levr., Dict. Sci. Nat. 29: 491. 1823; 38: 17. 1825. TYPE: *Wulffia baccata* (L.f.) Kuntze, Rev. Gen. Pl. 1: 373. 1891.

Woody *vines*, often high-climbing; stems terete or angled, puberulent or scabrous. *Leaves* opposite, ovate, shallowly toothed, coriaceous, glabrate or scabridulous, pinnately veined but successively 3–5-veined from near the base; petioles slender, forming a persistent intrapetiolar ridge. *Inflorescence* a terminal aggregate of several heads, these sometimes dichasial or subumbellate; bracts often present. *Heads* radiate, showy; involucre of numerous bracts in 2–3 imbricate series, ovate, indurate, sometimes recurving apically; receptacle convex; paleas indurate, stramineous, enfolding the florets, apically thickened; ray florets in 1 series, the corolla yellow, mostly narrow, denticulate, the tube short, the limb elongate; disc florets numerous, 5-merous, the corolla obconical, the tube short, the anthers with obtuse appendages, basally auriculate, the style branches lanceolate, unappendaged, the ovary strongly 3–4-angled, the pappus of one deciduous awn arising from an angle of the achene. *Achene* blackish, prismatic, plump, the pericarp thick, soft and fleshy, the endocarp black, hard; carpopodium small, yellowish; pappus absent at maturity.

Wulffia differs from *Melanthera* in the soft thickening of inulin materials in the pericarp of the achene and in the sclerified, thickened tips of the paleas. While Panamanian species of *Melanthera* are white flowered and lack rays, some species from South America have yellow rays and resemble *Wulffia*. *Wulffia* is also superficially similar to some species of *Zexmenia*, but these particular species have prominent awns on the achenes. *Wulffia* consists of one species ranging through

Central America and northern South America and several species from ultramontane South America.

The black fruits are held high at the edges of the forest and are eaten by birds which presumably digest the pericarp and pass through the hard seeds unscathed.

Literature:

Huber, J. 1898. Observaçoẽs histologicas e biologicas sobre o fruto da *Wulffia stenoglossa* DC (Jambú). Bol. Mus. Paraense Hist. Nat. 2: 96–101.

Schulz, O. E. 1911. Compositarum genera nonnulla. In I. Urban, Symb. Ant. 7: 78–144.

1. **Wulffia baccata**[50] (L. f.) Kuntze, Rev. Gen. Pl. 1: 373. 1891.—FIG. 77.

Coreopsis baccata L. f., Suppl. Pl. 380. 1781. TYPE: (LINN 1026.7).
Wulffia platyglossa DC., Prodr. 5: 563. 1836. TYPE: not seen.

Large woody *vine*, mostly high climbing; stems at first quadrate, soon terete, scabridulous with minute, white appressed hairs, often mottled. *Leaves* opposite, ovate, to 15 cm long, coriaceous, apically acuminate, basally obtuse or rounded, the margins crenate-dentate, the teeth callose tipped, pinnately veined with 1–2-pairs of strong veins diverging successively near the base, both sides scabridulous with scattered, small appressed, verrucose hairs, appressed pubescent on the major veins; petiole slender, to 15 mm long, the slender wings upfolded, the bases united in an interpetiolar ridge. *Inflorescence* a terminal aggregate of few–several heads, sometimes disposed in dichasial or subumbellate groups; bracts foliaceous; pedicels stout, deeply furrowed, scabrid, to 4 cm long, sometimes with a solitary bracteole along the length. *Heads* radiate, showy, globose, 1.2–1.8 cm across (not counting ray corollas); involucral bracts numerous in 1–3 similar but unequal series, 3–4 mm long, 2–4 mm wide, obovate, green to stramineous, indurate, often recurved apically, callose-mucronulate, the basally impressed midvein flanked by two sometimes elevated veins, dorsally puberulent; receptacle convex; paleas conspicuous, ca. 6 mm long, stramineous, indurate, enfolding the florets, the apex callose-sclerified into a thick, pointed umbo, strongly nerved, ciliate on the margins and costa; ray florets several in one series, the corolla orange or yellow, the tube short, flattened, the limb 10–15 mm long, ca. 4 mm wide, denticulate, the staminodes and style wanting, the ovary sterile, rudimentary; disc florets numerous, ca. 7 mm long, the corolla yellow, the tube short, the limb opening gradually upwards, ca. 4 mm long, the lobes obtuse, papillose-ciliate, the anthers black, ca. 2 mm long, the appendages yellow, the base auriculate, the style branches lanceolate, unappendaged, pilose, the style base not expanded, the nectary large, ca. 0.2 mm tall, cupular, apically sinuate, sometimes green, the ovary prismatic, with one short, stout, early deciduous awn arising from one of the angles. *Achene* black, ca. 5 mm long, prismatic, plump, the pericarp soft, fleshy, the endocarp black, flinty, apically surmounted by a small peg (the nectary); epappose.

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[50] A list of synonyms was published by Schulz (1911). Only the two names appearing here have been applied to Panamanian plants.

FIGURE 77. *Wulffia baccata* (L.f.) Kuntze. Habit (× ½). [After *Croat 6419* (MO).]

Wulffia baccata is widespread in tropical America, and is frequent in lowland Panama, the showy heads emerging at forest edges and from trees in fencelines. Immature herbarium specimens are sometimes mistaken for *Melanthera*, and mature specimens are sometimes taken for *Zexmenia virgulta* which differs in its pinnately-veined, puberulent leaves and shorter, broader involucral bracts.

BOCAS DEL TORO: Water Valley, *Wedel 753* (MO, US), *832* (GH, MO). Near Chiriquí Lagoon, *Wedel 1086, 1238* (both GH, MO), *2632* (GH, MO, NY, US). CANAL ZONE: Near Albrook Tower, *Blum 437* (US). Pipeline Road just N of Gamboa gate, *D'Arcy & D'Arcy 6017* (MO). Madden Forest S of Río Pedro Miguel, *D'Arcy 6100* (MO). Fort Kobbe, *Duke 3936* (GH, MO, US). Fort Sherman, *Dwyer 4358* (GH, MO). Coco Solo, *Dwyer & Duke 7900* (MO). Military road K-9, *Ebinger 538* (MO). Coco Solo, *Elias & Kirkbride 1610* (GH, MO). Gatún Station, *Hayes 69* (GH), *249* (NY). N of Frijoles, *Standley 47420* (US). Old Fort San Lorenzo, *Tyson 1547* (MO). 1 mi N of Summit Garden, *Tyson & Blum 1957* (MO). BARRO COLORADO ISLAND: Aviles *86* (MO); *Bailey & Bailey 477* (GH); *Bangham 482* (GH);

Croat 4224, 4267, 4371, 5961, 5980, 6009, 6082, 6137, 6363, 6378, 6419, 9123, 9291, 11466, 11772 (all MO), *16547* (MO, NY); *Dwyer 1426*; *Ebinger 138, 617* (both MO); *Kenoyer 375* (US); *Shattuck 36* (A, MO), *987* (MO, US); *Standley 10469* (US); *Starry 2, 182* (both MO); *Wetmore & Abbe 96* (A, GH, MO). COCLÉ: N of El Valle, 1000 m, *Allen 3686* (GH, MO). Hills above El Valle de Antón, *D'Arcy 6760* (MO). COLÓN: Santa Rita Ridge, *D'Arcy & D'Arcy 6143* (MO). Portobelo, *Dwyer 4397, 4398* (both MO). Fató, *Pittier 3861* (GH, NY, US), *4245* (GH, US). Santa Rita Ridge, *Gentry 9369* (MO). DARIÉN: La Boca de Pirre, *Bristan 1284* (MO). Río Pirre, *Croat & Porter 15525* (MO). Río Tuira, 5–15 mi below El Real, *Duke 4952* (GH, MO, US). Path from Pucro to Río Pucro, *Duke 5358* (MO). Río Sambú above Río Venado, *Duke 9263* (US). Loma-Cuasí behind Manené, *Duke 13636* (MO). Cerro Pirre, 2500–4500 ft, *Duke & Elias 13806* (MO). Santa Fe, *Duke 14284* (MO). Río Chucunaque above Río Tuquesa, *Stern et al. 852* (GH, MO, NY, US). HERRERA: 10 mi S of Ocú, *Tyson et al. 2829* (MO). PANAMÁ: Panama National Hwy. near Río Pacora, *Bartlett & Lasser 16948* (MO). Near Cerro Azul 3 mi above Goofy Lake, *Croat 11578* (MO). Road to Cerro Azul, 1000 ft, *D'Arcy & D'Arcy 6216* (MO). Cerro Jefe, *D'Arcy & D'Arcy 6262* (MO). Near Jenine, Río Cañita, *Duke 3802* (MO). Ca. 6 mi E of Chepo, *Duke 4066* (MO). Halfway between El Llano and Río Mamoní, *Duke 5602* (MO). Cerro Jefe, *Duke 9406, 9418* (both MO). Between Cañasas and Sabalo, 100 m, *Duke 14465* (MO). Tocumen, *Dwyer 4233* (US). Cerro Jefe, 2900 ft, *Dwyer & Gauger 7330* (GH, MO, US). Río Maestro, *Gentry 2208* (MO). Icantí, Río Agua Clara, *Gentry 2610* (MO). Without locality, *Hayes 74* (NY). Gatun Locks and Gatun Lake, *Johnston 1660* (GH, MO). S slope of Cerro Azul, *King 5253* (US). Cerro Jefe below summit, *Kirkbride & Crebbs 22* (MO, NY). 5 mi SW of Cerro Brewster, *Lewis et al. 3519* (MO). Cerro Azul, 2000 ft, *Tyson 2102* (MO). Road from Cerro Azul to Cerro Jefe, 2400 ft, *Tyson 6316* (MO). SAN BLAS: SW of Puerto Obaldía, *Croat 16763* (MO). Ailigandí, *Dwyer 6821* (MO). Mainland opposite Playon Chica, *Gentry 6401* (MO).

76. ZEXMENIA

Zexmenia La Llave in La Llave & Lexarza, Nov. Veg. Descr. 1: 13. 1824. TYPE: *Z. serrata* La Llave.

Herbs or widely branched *shrubs*, sometimes scrambling; stems slender, pubescent. *Leaves* opposite, ovate or lanceolate, entire or denticulate, often pinnately veined, pubescent, sometimes coriaceous; petioles pubescent, canaliculate above. *Inflorescence* an open panicle, sometimes cymose; bracts or bracteoles sometimes alternate. *Heads* radiate; involucral bracts in several series, the outermost narrower, the inner series ovate, basally indurate; paleas scarious, enfolding the florets; ray corollas mostly yellow, the limb narrow, denticulate, the ovary fertile, 3-angulate, 3-awned; disc corollas tubular, 5-merous, the lobes short, porrect, dorsally pubescent, the anthers appendaged, basally subauriculate, the ovary fertile, laterally flattened, apically winged, two awns departing centrifugally from near the center of the apex, then bending upwards, a small squamellate pappus sometimes present. *Achenes* dark, glabrous, apically winged, with two stout awns arising from near the center of the summit, bending first outwards and then upwards; pappus of small scales sometimes present between the awns.

Zexmenia includes 3–4 species of Central America which are closely related to species of *Wedelia* and *Oyedaea*. Only one species occurs in Panama.

1. **Zexmenia virgulta** Klatt, Bull. Soc. Roy. Bot. Belgique 31: 203. 1892. TYPE: not seen.—FIG. 78.

Scrambling *shrub*; twigs slender, drying longitudinally striate, tomentose with fine hairs and stout, ascending white hairs, glabrescent. *Leaves* opposite, to 15

FIGURE 78. *Zexmenia virgulta* Klatt.—A. Habit (× ½).—B. Achene (× 3½). [After *Busey* 659 (MO).]

cm long, chartaceous to subcoriaceous, ovate to lanceolate, apically acute or acuminate, basally obtuse, the margins serrulate, the veins pinnate, ca. 5 on each side of the midrib, drying darker above, scabridulous, soft tomentose beneath; petioles mostly 8–10 mm long, tomentose, canaliculate above. *Inflorescence* an

open panicle with few or many heads, umbelliform; bracts foliaceous, opposite; bracteoles subfoliaceous or scalelike, sometimes alternate on the peduncles or associated with the heads and forming an outer whorl of involucral bracts. *Heads* compressed-globose; involucre ca. 1.5 mm across, the outermost bracts 4–10 mm long, apically or entirely oblong-lanceolate, green, somewhat recurving, the inner series broader, mostly shorter, ovate, basally indurate, dorsally appressed pubescent, ciliate; paleas 6 mm long, scarious, apically pubescent, enfolding the floret; ray florets ca. 12 in one series, the corolla yellow, the ligule ca. 5 mm long, ovate, minutely denticulate, glabrous, the tube glabrous, ca. 5 mm long, the style branches small, ovary fertile, 3-awned; disc florets numerous, 8 mm long, the corolla yellow, 6 mm long, the tube lighter, glabrous, forming almost half the length, apical lobes puberulent dorsally, the anthers dark with dark appendages, basally auriculate, the style branches ascending-pilose with a minute appendage, the stigmatic lines running the full length of the branches, the style base not expanded, inserted in a narrow, cylindrical, apically irregular, 1 mm long nectary, the ovary fertile, strongly laterally compressed, the angles long-pilose, slightly constricted apically with two stout, ascending-strigose awns which exceed the corolla, the pappus of a ring of squamellae. *Achene* bodies black, ca. 3 mm long, surrounded by corky, 1 mm thick, sparingly pilose wings, and surmounted by the squamellate pappus and sometimes by one or two weak awns.

The achene of this species resembles that of some species of *Wedelia*, but the organization of the involucre is quite different. This species is known also from Costa Rica. Herbarium material may be mistaken for *Wulffia baccata*, which has slightly shiny, less pubescent leaves, and leaves more strongly 3–5-nerved from near the base.

BOCAS DEL TORO: Changuinola Valley, *Dunlap 410* (US). CHIRIQUÍ: 30 km N of Paso Canoas, 600 m, *Busey 621* (MO). 2–8 km N of Cañas Gordas (Costa Rica), 1000–1100 m, *Busey 659* (MO). Along road to Cerro Punta, *King 5291* (US). Near San Félix, *Pittier 5455* (US). El Valle, *Allen 749* (US). W facing slopes of El Valle, *King 5323* (US). Between Margaritas and El Valle, *Woodson et al. 1748* (US). PANAMÁ: Cerro Campana, *Ebinger 372* (US). SW slopes of mountains W of Chica, *King 5262* (US). VERAGUAS: Hills W of Soná, *Allen 1038* (US). Highway to Soná, *King 5282* (US).

F. COREOPSIDINAE

W. G. D'Arcy[51]

Coreopsidinae Less., Linnaea 5: 153. 1830. "Coreopsideae." TYPE: *Coreopsis* L.

Coreopsidaceae Link, Handb. 1: 768. 1829. "Coreopsideae." TYPE: *Coreopsis* L.
Trichospirinae Less., Linnaea 6: 690. 1831. "Trichospireae." TYPE: *Trichospira* H.B.K.

Literature:

Sherff, E. E. 1955. Subtribe Coreopsidinae. *In* E. E. Sherff & E. J. Alexander. North American Flora, ser. 2, 2: 1–190.

[51] Missouri Botanical Garden, 2315 Tower Grove Avenue, St. Louis, Missouri 63110.

77. BIDENS[52]

Bidens L., Gen. Pl., ed. 5. 362. 1754. TYPE: *B. tripartita* L.

Pluridens Neck., Elem. Bot. 1: 86. 1790, nom. mut. *Bidens* L.
Edwardsia Neck., Elem. Bot. 1: 1790, nom. mut. *Bidens* L.
Kerneria Moench, Meth. 595. 1794. TYPE: *K. trigona* Moench = *Bidens pilosa* L.
Ceratocephalus Cass., Dict. Sci. Nat. 7: 432. 1817. TYPE: *Bidens pilosa* L.
Delucia DC., Prodr. 5: 633. 1836. TYPE: *D. ostruthioides* DC.
Diodonta Nutt., Trans. Amer. Phil Soc., n.s. 7: 360. 1841. LECTOTYPE: *D. leptophylla* Nutt. = *Bidens mitis* (Michx.) Sherff.
Diadonta Walp., Repert. Bot. Syst. 2: 614. 1843, orth. mut. *Diodonta* Nutt.
?*Acocotli* Hernandez, Altam. Mat. Med. Mex. 2: 154. 1898, cf. Sherff, N. Amer. Flora, ser. 2, 2: 113. 1955.

Herbs, perennial or annual, erect, scandent or procumbent, rarely shrubby or paludal; stems mostly pubescent and drying striate or sulcate, at least when young. *Leaves* opposite, simple or compound, serrate, lobed or dissected, rarely entire, mostly petiolate. *Inflorescences* of solitary, sometimes aggregated terminal heads; peduncles slender, narrowing upwards, striate, subtended by paired, foliaceous bracts and often by one or more alternately disposed foliaceous or scalelike bracteoles along their length. *Heads* mostly radiate, sometimes showy; involucre of an outer series of distinct, herbaceous, acute or rarely foliaceous bracts and an inner series of broader, membranous, sometimes basally united bracts, the margins often hyaline; receptacle flat or convex; paleas resembling the inner involucral bracts but narrower, slightly curved around the ovary; ray florets few–many in 1 series or wanting, the corolla with a broad, apically denticulate limb, drying with longitudinal nerves, the tube short, the ovary sometimes fertile; disc florets numerous, the corolla tubular, the 5-lobes yellowish, glabrous or puberulent on the ventral surface, the anthers often black, basally obtuse or subauriculate, the appendages large, the style branches flattened, apically pilose with a short, narrow appendage, the ovary mostly fertile. *Achenes* black or brown, narrowly fusiform or linear, sulcate, often apically ascending-strigose, mostly surmounted by 1–6 retrorsely strigose awns held at various angles, those of the marginal disc florets sometimes different from those of the central disc florets, those of the rays sometimes flattened, broad.

Bidens is a genus of about 75 species mainly of Mexico but ranging into North and South America. Several species are widely naturalized as weeds. It is closely related to *Coreopsis* and *Cosmos*.

Literature:

Sherff, E. E. 1937. The genus *Bidens*. Field Mus. Nat. Hist., Bot. Ser. 16: 1–709.

a. Plant erect, annual; ray florets not showy, yellow or white, less than 12 mm long, or wanting.

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[52] Assistance from T. Melchert, University of Iowa, in preparing the treatment for *Bidens* is gratefully acknowledged.

b. Leaves 3(–5)-foliolate, the leaflets serrate; achenes straight.
c. Achenes less than 12 mm long, the awns erect ---------- 3. *B. pilosa*
cc. Achenes more than 12 mm long, the awns divaricate, sometimes reflexed ---------- 5. *B. riparia* var. *refracta*
bb. Leaves 2–3-pinnately divided, the leaflets deeply toothed or lobed; achenes curved ---------- 1. *B. bipinnata* var. *cynapiifolia*
aa. Plants procumbent, ascending or scandent, not erect, perennial; ray florets showy, yellow or orange, more than 12 mm long.
d. Plants scandent, the shoots more than 45 cm long; the solid portions of the leaf blade more than 10 mm wide, the margins serrate ---------- 4. *B. reptans*
dd. Plants procumbent, rooting at the lower nodes, the ascending shoots less than 30 cm long; the solid portions of the leaf blade less than 10 mm wide, the margins deeply toothed or lobed.
e. Ray florets fertile; style branches conspicuous in living material ---------- 2. *B. ostruthioides* var. *costaricensis*
ee. Ray florets sterile; style branches mostly wanting ---------- 6. *B. triplinervia*

1. **Bidens bipinnata** L., Spec. Pl. 832. 1753. TYPE: not seen.

1a. **Bidens bipinnata** var. **cynapiifolia** (H.B.K.) Maza, Anales Soc. Esp. Hist. Nat. 19: 275. 1890.

Bidens cynapiifolia H.B.K., Nov. Gen. Sp. Pl. 4: 235. 1820. TYPE: Cuba, Guanavaca, *Bonpland 1562* (P).

Erect, branched annual *herb* to 1.5 m tall; stems glabrate, drying conspicuously many-ribbed. *Leaves* opposite, pinnate or bipinnate, to 15 cm long (including petiole), leaflets apically acuminate or acute, basally cuneate to truncate, the margins mostly saliently toothed, ciliate in part, puberulent above and beneath with short hairs, venation pinnate; petiole slender, glabrate. *Inflorescences* solitary heads or a paniculate aggregation of heads involving upper portions of the plant; peduncle slender, to 12 cm long, glabrate; bracts small, compound; bracteoles when present solitary on the peduncle, linear. *Heads* radiate, sometimes inconspicuously so; involucral bracts in 2 dissimilar series, the outermost ca. 8, linear, expanded apically and basally, apically obtuse or rounded, glabrate, drying 1- or 3-nerved, ca. 5 mm long, the innermost lanceolate, glabrous, conspicuously dark-striate, the margins hyaline; receptacle pilose; paleas resembling the innermost series of involucral bracts but narrower; ray florets several or wanting, the corollas yellow, the limb broad, drying strongly 5–7-nerved, apically entire or minutely emarginate, the tube flat, 1.5 mm long, glabrous; disc florets numerous, 5–6 mm long, the corolla tube 1 mm long, ?angled, the limb cylindrical, conspicuously dark-nerved, the 5 lobes glabrous with dark nerves, the anthers ca. 1.5 mm long, dark, the appendages dark, the basal auricles small or wanting; style branches flattened, lanceolate, dorsally pilose, with a slender apicule, the style base not expanded, immersed in the 1 mm tall, cylindrical nectary, the ovary compressed, the margins sparingly pubescent near the apex, the pappus of ca. 6 awns, each with a dark costa. *Achene* dark, ca. 12 mm long, slightly curved, angled, glabrous, with ca. 6 stout, erect, retrorsely barbed awns, those of the margin shorter, ascending-tomentose.

This erect species may be recognized by the usually bipinnate leaves which are not divided into narrow segments as in *B. ostruthioides*. The achenes are dimorphic; the majority of the innermost are glabrous but a few at the margin are densely tomentose.

Variety *cynapiifolia* ranges through the Antilles and Central America. It is reported from South America and is adventive in Hawaii and in the Old World. It is a weedy species of lowlands.

Bidens bipinnata L. var. *bipinnata* of the southeastern United States differs from var. *cynapiifolia* in having usually straight achenes with less differentiation between those of the margin and those of the center.

CANAL ZONE: Mount Hope Cemetery, *Standley 28804* (US). Farfan Beach area, *Tyson & Blum 2610* (MO). COCLÉ: Aguadulce, *Pittier 4839* (US). PANAMÁ: Peña Prieta, *Heriberto 251* (US). E of Río Tocumen, *Standley 26646* (US). Near Juan Franco race track, *Standley 27799* (US). Nuevo San Francisco, *Standley 30741* (US).

2. **Bidens ostruthioides** (DC.) Schultz-Bip. in Seem., Bot. Voy. Herald 308. 1856.

2a. **Bidens ostruthioides** var. **costaricensis** (Benth. in Örst.) Sherff, Bot. Gaz. (Crawfordsville) 88: 298, *pl. 21*. 1929.

B. costaricensis Benth. ex Örst., Vidensk. Meddel. Dansk Naturhist. Foren. Kjøbenhavn 1852: 94. 1852. TYPE: *Oersted 137* or *183* (K, mounted on same sheet).

Perennial *herb* to 40 cm tall, glabrate; stems terete, drying strongly angled, reclining, rooting at the nodes, new growth ascending. *Leaves* 2–3-pinnately lobed, the segments acute or obtuse, mucronulate, to 10 cm long, 2–10 mm broad, drying with the venation prominent beneath; petiole slender, often narrowly winged, to 4 cm long, slightly expanded and ciliate at the base. *Inflorescences* of 1–3-terminal heads; peduncles slender, narrowing upwards, to 20 cm long; mostly ebracteolate but sometimes with one or two entire bracteoles along the length. *Heads* radiate, showy; outer involucral bracts ca. 5, distinct, glabrate, ca. 8 mm long, 4 mm wide, herbaceous, apically acute, basally contracted and thickened, the inner bracts membranaceous, shorter or longer than the outer bracts, basally puberulent; ray florets yellow, showy, the corollas 2–3 cm long, 10–15 mm wide, longitudinally veined, minutely 3-denticulate, the teeth acute, the style slender, 4–5 mm long, exserted, the branches slender, slightly compressed, granular, not pubescent, the ovary fertile; disc florets numerous, the corolla yellowish, glabrous outside, the lobes minutely puberulent on the ventral surface, the anthers black, the style branches expanded-truncate with conical, pilose appendages. *Achene* (after Sherff) pale brown, narrow, 7–9 mm long, glabrous with 2–4 retrorsely barbed awns 3.5–5 mm long.

This species closely resembles *Bidens triplinervia* but is slightly larger in habit and leaves and the ray florets are fertile. The sole Panamanian collection is in poor condition and is referred to this species with hesitation. However, as the species has been collected in neighboring Costa Rica, it is a likely member of the

Chiriquí mountain flora. The above description is taken mainly from a series of Costa Rican collections. Thomas Melchert has mentioned verbally that in living material the styles of the ray flowers are a conspicuous feature distinguishing *B. ostruthioides* from *B. triplinervia*. *Bidens ostruthioides* var. *ostruthioides* has trifoliolate, hardly dissected leaves.

CHIRIQUÍ: Cerro Pando, valley of the upper Río Chiriquí Viejo, *White 48* (MO).

3. **Bidens pilosa** L., Sp. Pl. 832. 1753. TYPE: America, Herb Linn. (LINN 975.8).

B. leucantha Willd., Sp. Pl. 3: 1719. 1803.

Erect, branched, annual *herb* to 1.5 m tall; stems angled, green, glabrate. *Leaves* opposite, 3(–5)-foliolate, the leaflets to 7 cm long, ovate, apically acute, obtuse or acuminate, basally acuminate to truncate, the margins serrate, pinnately veined, reticulate beneath, puberulent on both sides, the hairs longer beneath; petiole slender, basally expanded and slightly clasping, the basal margins ciliate. *Inflorescence* mostly of several loosely aggregated, terminal heads; peduncle to 5 cm long, slender, erect, glabrate or puberulent, drying angled. *Heads* radiate or discoid; involucre 5–8 mm high, the bracts in 2 dissimilar series, the outer series narrow, herbaceous, expanded basally and apically, only the basal expansion imbricate, 1-nerved, the apex ciliate, obtuse or rounded, the inner series ovate, indurate, obscurely or conspicuously several-nerved, the margins scarious-hyaline; receptacle flat; paleas wanting; ray florets several in 1 series or wanting, the corolla white or yellow, 7–12 mm long, the tube short, dorsiventrally flattened, ciliate on the margins, the limb ovate, sometimes broadly so, 2-notched, drying prominently 5–7 nerved, the style present or not, the ovary sterile, faintly trigonous; disc florets numerous, the corolla yellowish or greenish, 3–4 mm long, sparingly stipitate-glandular, the tube ca. 1 mm long, the limb narrowly obconical, the 5 lobes dorsally pilose, the anthers black, ca. 2 mm long, with ovate, eglandular appendages, the basal auricles indistinct, the style branches flattened, lanceolate, pilose, with a linear apicule, the style base not expanded, immersed in a 0.5 mm long, cylindrical nectary, the ovary compressed, weakly 4-angled, pilose with ascending hairs, glandular-stipitate near the apex, the pappus of two stout retrorse-strigose awns. *Achene* black, 15–22 mm long, linear, strongly angled, glabrous but with a few stiff, short, ascending hairs near the apex; carpopodium oblique, stramineous, puberulent; pappus of 2–3 stiff, retrorsely strigose awns (aristae), ca. 3 mm long.

This species is native to the Caribbean region but is widespread as a weed of tropical and warm temperate lands. It may be recognized by its usually trifoliolate, serrate-margined leaves and by its black, straight, 3-awned, linear achenes. The awns are erect. It is the only species of *Bidens* in Panama which sometimes produces white-rayed heads. "Spanish Needles."

A number of varieties and forms have been recognized under this species, T. Melchert has indicated that probably none of these is of taxonomic significance.

Panamanian plants which have reduced rays (most collections) may be referred to as f. *minor* Sherff.

BOCAS DEL TORO: Above railroad station at mi 7.5, *Croat & Porter 16426, 16438* (both MO). Changuinola, *Stork C36* (UC). Without definite locality, *Wedel 158* (GH, MO). CANAL ZONE: Pedro Miguel, *Heriberto 103* (US). Monte Lirio, *Maxon 6850* (US). Ancón Hill, *Piper 5545* (US). Juan Mina, *Piper 5706* (US). Balboa, *Standley 27004* (US). Frijoles, *Standley 27630* (US). Gamboa, *Standley 28473* (US). France Field, *Standley 28592* (US). Near Summit, *Standley 29995* (US). Darién Station, *Standley 31533* (US). Near Salamanca Hydrographic Station, Río Pequeni, *Woodson et al. 1610* (US). Darién Station, *MacBryde 2683* (F, US). CHIRIQUÍ: 19 km W of Puerto Armuelles, 500 m, *Busey 608* (MO). El Hato del Volcán, *Croat 10404* (MO). Between Boquete and Monte Rey, *Croat & Porter 15649* (MO). Cerro Pando, *D'Arcy & D'Arcy 6321* (MO). Roadside W of Cerro Pando, ca. 6000 ft, *D'Arcy & D'Arcy 6636* (MO). Near Boquete, 3300–4200 ft, *Lewis et al. 422* (MO). Valley of the upper Río Chiriquí Viejo near Monte Lirio, 1300–1900 m, *Seibert 233* (MO). Collins Finca, Boquete District, 6000 ft, *Ebinger 697* (F). Interam. Hwy. at Concepción, *King 5287* (UC, US). Near Boquete, *Maurice 686* (US). Alto Boquete, *Partch 69-135* (MO). Cerro Punta, *Sawyer*, 1 March 1967 (MICH). Upper Río Chiriquí Viejo near Monte Lirio, *Seibert 232* (MO), *233* (GH, NY). Bambito, 5600 ft, *Tyson 5635* (MO). COCLÉ: El Valle de Antón, *D'Arcy & D'Arcy 6716* (MO). PANAMÁ: S slopes of Cerro Azul, *King 5245* (UC, US). Las Sabanas, *Paul 18* (US). Cerro Jefe, *Tyson et al. 4299* (MO). VERAGUAS: 15 mi N of Calobre, 644 m, *Luteyn 1449* (MO).

4. **Bidens reptans** (L.) G. Don in Sweet, Hort. Brit., ed. 3. 360. 1839.—FIG. 79.

Coreopsis reptans L., Syst. Nat., ed. 10, 2: 1228. 1759. TYPE: Jamaica, *P. Browne* (LINN 1026.13).
Bidens squarrosa H.B.K., Nov. Gen. Sp. Pl. 4: 187. 1820. TYPE: Venezuela, *Humboldt & Bonpland* (P, not seen).
?*B. segetum* Mart. ex Colla, Herb. Pedem. 3: 307. 1834. TYPE: Brasil, *Martius* (TO, not seen).
B. tereticaulis DC., Prodr. 5: 598. 1836. TYPE: not seen.

Large, scandent *herbs*, often clambering in thickets to 3 m high; stems glabrate, fistulose, sometimes stout. *Leaves* opposite, trifoliolate, the leaflets to 10 cm long, ovate or lanceolate, apically acuminate, basally obtuse, the margins serrate, pinnately veined, sometimes drying reticulate beneath, puberulent on both sides with weak hairs; petioles glabrate or puberulent, slightly expanded and clasping at the base. *Inflorescence* a racemose-paniculate aggregation of flowers along the ends of the branches; peduncles glabrate or pubescent, slender, to 11 cm long; bracts short, linear-spatulate; linear-spatulate bracteoles sometimes present. *Heads* radiate, showy, to 4 cm across; involucral bracts in 2 dissimilar series, the outermost narrow, to 6 mm long, expanded basally and apically, imbricate only at the basal expansion, drying 3-nerved, ciliate, sometimes pubescent at the base, the innermost series lanceolate, indurate, the margins hyaline-scarious, apically thickened and tomentose; paleas lanceolate, scarious, apically dark-striate and puberulent; ray florets 4–7, the corolla showy yellow, to 2.5 cm long, the tube 2–3 mm long, flattened, sparsely pilose, the limb narrow, glabrate, drying prominently 10–12-nerved, apically mucronulate or minutely denticulate, the style mostly wanting, the ovary sterile, flat; disc florets numerous, 8–10 mm long, the corolla 5–6 mm long, the tube ca. 1.5 mm long, glabrate, the limb tubular, the lobes glabrous, the anthers black, ca. 3 mm long, the appendages ovate, dark, the base subauriculate, the style branches flattened, ventrally pilose with a thick

A
B

apicule, the style base not expanded, immersed in a 1 mm long, cylindrical nectary, the ovary flattened, pilose on the margins. *Achene* dark, 12–16 mm long, linear, flattened, ascending-pilose on the angles and at the apex; the two awns erect, retrorsely strigose.

This species is recognizable by its showy yellow heads, its scandent habit, and its dark, linear, marginally pubescent achenes which usually bear two stout apical awns.

Bidens reptans ranges through the moist uplands of tropical America. In Panama it is found mainly in the Chiriquí mountains but one collection comes from Cerro Azul which does not reach 1,000 m.

Bidens segetum appears to refer to unusually pubescent plants of *B. reptans* such as *Allen 4864* from Panama.

CHIRIQUÍ: Near New Switzerland, 1800–2000 m, *Allen 1342* (F, MO, US). N face of Cerro Copete, an eastern spur of Chiriquí Volcano, 8000–8500 ft, *Allen 4864* (MO). Cerro Punta, ca. 7000 ft, *Blum et al. 2404* (MO). Las Nubes, 5.5 km NW of Río Chiriquí Viejo, 2200 m, *Busey 682* (MO). Trail north of Cerro Punta, *Croat 10482* (MO). Palo Santo, 3 mi N of Volcán, *Croat 13542* (MO). Between Cerro Punta and Bajo Grande, *Croat & Porter 16010* (MO). 10–11 mi W of Puerto Armuelles, near San Bartolo Limite, 300–500 m, *Croat 22001* (MO). Above Cerro Punta on slope of Cerro Respinga, 8000 ft, *D'Arcy & D'Arcy 6532* (MO). Bajo Chorro, Boquete District, 6000 ft, *Davidson 151* (F, MO). Volcán de Chiriquí, 9500 ft, *Davidson 1004* (F). Río Chiriquí Viejo N of Volcán City, 5200–5600 ft, *Duke 9070* (MO). Boquete, 6000 ft, *Ebinger 690, 693* (F, MO). Near Boquete, *Lewis et al. 314, 580* (both MO, US). NE of Alto Linio, 4300 ft, *Maurice 862* (F, MO, UC, US). Volcán de Chiriquí, *Woodson et al. 806* (MO, US). COCLÉ: Hill S of El Valle de Antón, 600–800 m, *Allen 1177* (MO), *2854* (US, MO). PANAMÁ: Road between Cerro Azul and Cerro Jefe, 2400 ft, *Tyson 6318* (SCZ). VERAGUAS: 2 mi W of Santa Fe, 400–800 m, *Liesner 842, 843A* (both MO). Ca. 2 km N of Escuela Agrícola Alto de Piedra, N of Santa Fe, *Mori & Kallunki 2610* (MO).

5. **Bidens riparia** H.B.K., Nov. Gen. Sp. Pl. 4: 236. 1820, not *B. riparia* E. L. Greene, Pittonia 4: 261. 1901. TYPE: Colombia, Herb. H.B.K. (P, not seen, IDC 602. 109. III. 6).

5a. **Bidens riparia** var. **refracta** (Brandegee) O. E. Schulz, Symb. Ant. 7: 132. 1911.

B. refracta Brandegee, Zoe 1: 310. 1890. TYPE: Baja California, collection not designated.

Erect, branched *herb* to 1 m tall; stems sometimes stout, drying conspicuously striate, glabrate. *Leaves* opposite, mostly trifoliolate, occasional leaves 7-foliolate or bipinnate, to 7 cm long, leaflets mostly 2–3 cm long, ovate, apically acuminate, basally truncate to obtuse, serrate, pinnately veined, often reticulate beneath, sparingly pubescent with short weak hairs; petiole ca. ½ as long as the leaflet, slender, glabrate, slightly expanded and clasping at the base. *Inflorescence* an open aggregate of terminal and subterminal heads; peduncles to 10 cm long, striate, glabrate; bracts foliaceous; bractlets mostly 1 or 2, alternate, linear or

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FIGURE 79. *Bidens reptans* (L.) G. Don.—A. Habit (× ½).—B. Head (× 2). [After *Blum et al. 2404* (MO.)]

compound. *Heads* mostly radiate; involucral bracts in 2 dissimilar series, the outermost ca. 8, linear, ca. 5 mm long, green, glabrate, the innermost broadly lanceolate, membranous or indurate, dark, glabrous, the margins scarious imbricate; receptacle pubescent; paleas resembling the innermost involucral bracts but narrower; ray florets inconspicuous, the corolla ?yellow, the limb drying prominently 5–9-nerved, apically minutely notched, 3–4 mm long, the tube ca. 1 mm long; disc florets numerous, the corolla 4–5 mm long, the tube puberulent, the limb cylindrical, angled, the angles with prominent dark veins, the 5 lobes with dark nerves, glabrous, the anthers dark, basally subauriculate, the appendages narrow, ovate, dark, the style with 4 dark nerves, the branches flattened, apiculate, pilose, the style base immersed in the short, cylindrical, apically sinuate nectary, the ovary elongate, angled, pubescent, the pappus of ca. 4 stout, retrorsely strigose awns. *Achene* dark, linear, slightly outcurving, ca. 1.5 cm long, conspicuously striate, glabrous or puberulent apically; the outermost achenes densely tomentose with ascending hairs, pappus of ca. 4 stiff, spreading, retrorsely strigose, 3–4 mm long awns.

This species ranges through Central America and northern South America, occurring as a lowland weed of ruderal or disturbed situations.

B. riparia is distinct from *B. bipinnata* var. *cynapiifolia* to which it is closely related in its trifoliolate rather than pinnate leaves, its serrate rather than saliently toothed leaflets, and its larger achenes with relatively shorter awns. Although radiate, the head may appear disciform.

Sherff (1955) and Schulz (1911) recognized two varieties under *B. riparia*, the first writer because of the degree of division of the leaves, a feature which appears to vary on different parts of a single plant, and the second writer because of the degree of pubescence of the achenes.

CANAL ZONE: Balboa, *Standley 26078* (US). Near Gatún, *Standley 27332* (US). Near Juan Franco race track, *Standley 27800* (US). HERRERA: 10 mi S of Ocú, *Tyson et al 2836* (MO). LOS SANTOS: 3 mi S of Carreta, ca. 5 mi S of Las Tablas, *Burch et al. 1239* (MO). PANAMÁ: 1 mi E of Tocumen Airport, *Blum & Tyson 1963* (MO). Vera Cruz, *Lewis et al. 2997* (MO). Saboga Island, Pearl Islands, *Tyson & Loftin 5120* (MO).

6. **Bidens triplinervia**[53] H.B.K., Nov. Gen. Sp. Pl. 4: 182. 1820. TYPE: Mexico, *Humboldt & Bonpland* (P, not seen).

?*B. andicola* H.B.K., Nov. Gen. Sp. Pl. 4: 186. 1820. TYPE: Ecuador, *Humboldt & Bonpland* (P, not seen).
B. mollis Poepp. & Endlich., Nov. Gen. Sp. Pl. 3: 49. 1845. TYPE: Peru, *Poeppig 1377* (W, not seen).
B. humilis H.B.K. var. *macrantha* Wedd., Chlor. And. 1: 69. 1856. TYPE: Ecuador, *Jameson 55* (G, K, neither seen).
B. triplinervia var. *macrantha* (Wedd.) Sherff, Bot. Gaz. (Crawfordsville) 80: 383. 1925.
B. triplinervia var. *mollis* (Poepp. & Endlich.) Sherff, Bot. Gaz. (Crawfordsville) 80: 383. 1925.

Sprawling or ascending perennial *herb*, to 40 cm tall, sometimes much branched below; stems glabrous or pilose in lines, sometimes rooting at the lower nodes, the internodes short or long. *Leaves* opposite, to 4 cm long, deeply lobed, sometimes

[53] Other synonyms are presented by Sherff (1937: 506) but only the listed names have been used for Panamanian material.

trifoliolate or bi-compound, the sinuses narrow, the lobes 2–4 on each side, apically obtuse or acute, mucronulate, the basal half entire, acute; petiole short or to 7 mm long, basally ciliate. *Inflorescence* of 1–3 heads inserted between reduced, foliaceous bracts or branching from a common peduncle; peduncle slender, to 20 cm long, gradually narrowing upwards, sometimes with one or two bracteoles opposite or alternating along its length. *Heads* radiate, sometimes showy; involucral bracts in several series of about equal length, the outer series glabrate, 3 mm long, linear, apically rounded and mucronulate, the inner series dorsally pubescent at the base, broader, slightly longer; receptacle convex; paleas scarious, 7 mm long, the costa striate, the tip darkened; ray florets 5–8, the corolla yellow, broad, apically minutely 2–3-denticulate or entire, the venation prominent, 2–3 cm long, 1–1.5 cm wide, the style mostly wanting, the ovary sterile; disc florets numerous, the corolla yellowish, ca. 5 mm long, tubular, the limb expanded, tubular, the margins of the lobes thickened, papillose, the anthers ca. 2 mm long, yellowish, basally subauriculate, the appendages narrow, ligulate, the filaments glabrous, the style branches apically ascending-pilose with a short, papillose, linear appendix, the style base inserted in a cylindrical nectary, the ovary fertile. *Achenes* dimorphic, the outer series few, shorter, slightly incurved and dull, the innermost numerous, linear, deeply sulcate, black, shiny, mostly straight, glabrous or with a few minute ascending bristles near the apex; carpopodium yellowish; pappus of 2–4 short awns, retrorsely barbed, yellow, 1–2 mm long.

This species is known in Panama only from middle and upper elevations in the Chiriquí mountains. The small, toothed and deeply lobed, sometimes trifoliolate or bipinnate leaves, the showy yellow heads on long peduncles, plus the short, black, aristate needlelike achenes are distinctive. This species is quite similar to *Bidens ostruthioides* DC. which occurs in neighboring Costa Rica. *Bidens ostruthioides* is distinguished by its fertile ray florets and by its styles which are conspicuous on living material. It also has somewhat larger leaves, and the receptacle is glabrous.

CHIRIQUÍ: Llanos del Volcán, 1300 m, *Allen 1545* (MO). Potrero Muleto, Volcán de Chiriquí, 10400 ft, *Davidson 1008* (MO). Near Boquete, *Duke 9179* (US). Volcán de Chiriquí, 11960 ft, *Terry 1324* (MO). Top of El Barú, above 11000 ft, *Tyson & Lofton 6169* (MO). W slope of El Barú, 10000–11000 ft, *Tyson & Loftin 6152* (MO). Volcán de Chiriquí, 3500–4000 m, *Woodson & Schery 420* (MO).

78. CHRYSANTHELLUM

Chrysanthellum L. C. Rich. in Pers., Syn. Pl. 2: 1807. TYPE: *C. procumbens* L. C. Rich. = *C. americanum* (L.) Vatke.

Microlecane Schultz-Bip. ex Benth. & Hook., Gen. Pl. 2: 384. 1873. TYPE: *M. abyssinica* Schultz-Bip. = *Chrysanthellum americanum* (L.) Vatke.
Chrysanthellina Cass., Dict. Sci. Nat. 25: 390. 1822, orth. mut. *Chrysanthellum* L. C. Rich.
Collaea Spreng., Syst. Veg. 3: 622. 1826. TYPE: *C. procumbens* (L. C. Rich.) Spreng.
Sebastiana Bertol., Lucubr. 37. 1822. TYPE: S. *heterophylla* Bertol. = *Chrysanthellum americanum* (L.) Vatke.

Diminutive, short-lived *herbs*, erect, prostrate or ascending with a short, slender tap root. *Leaves* alternate or opposite, entire, dentate to bipinnately dissected with

fine divisions, glabrate; the petiole slender, sometimes not distinguished from the blade, slightly clasping the stem. *Inflorescence* of solitary ascending flowers or rarely clustered in an ill-defined panicle; peduncle slender, glabrate, often with foliaceous or scalelike bracts. *Heads* radiate; involucral bracts in 2–3 dissimilar series, the outer bracts few, short, linear to lanceolate and conspicuously basally thickened, the inner series similar, imbricate, the innermost sometimes slightly narrower, imbricate, oblong to lanceolate, indurate or chartaceous, drying striate, the hyaline margins broad, entire; receptacle hemiglobose; paleas mostly persistent, linear with a dark costa and hyaline margins, the outermost half enfolding the ray ovaries; ray florets several in ca. 2 series, the corolla yellow with a short tube and two distinct longitudinal ribs, apically 2(3)-denticulate, the ovary laterally flattened, epappose; disc florets several, the corolla campanulate, the 5 lobes enervate, glabrous, the anthers dark with deltoid, uncolored appendages, basally obtuse or subauriculate, the style branches with flattened, pilose margins. *Achenes* often dimorphic, the outermost oblong, buff, tuberculate, sometimes puberulent, the apex slightly expanded into two lateral ears, the innermost flat, black, with massive, light-colored wings; pappus wanting.

This is a genus of perhaps 6 species in the tropics of both the New and Old Worlds. The dimorphic involucral bracts, and the prominently winged, epappose, central fruits are distinctive. This is a genus where the term palea requires broad definition, for the bracts enfolding the ray ovaries and those subtending the disc ovaries are alike but different from the two types of involucral bracts.

1. **Chrysanthellum americanum** (L.) Vatke, Abh. Naturwiss. Vereine Bremen 9: 122. 1885.

Anthemis americanum L., Sp. Pl. 895. 1753. TYPE: Jamaica, Hort. Cliff. (BM, not seen). Protologue cites also Sloane, Voy. Isl. Madera 1: 263, *tab. 155, fig. 3.* 1707. TYPE: Jamaica, *Sloane* (BM, not seen).

Bidens apiifolia L., Syst. Nat., ed. 10. 1203. 1759. Based on Sloane, Voy. Isl. Madera 1: 263, *tab. 155, fig. 3.* 1707.

Verbesina mutica L., Sp. Pl., ed. 2. 1273. 1763. TYPE: Jamaica, *Houston 1732* (LINN 1020.10 ex herb Gronov.).

Chrysanthellum procumbens L. C. Rich. in Pers., Syn. Pl. 2: 471. 1807. Based on *Verbesina mutica* L.

Sebastiana heterophylla Bertol., Lucubr. 37. 1822. TYPE: not seen.

Collaea procumbens (L. C. Rich.) Spreng., Syst. Veg. 3: 622. 1826.

1a. **Chrysanthellum americanum** var. **integrifolium** (Steetz) Alexander, N. Amer. Flora, ser. 2, 2: 148. 1955.—Fig. 80.

C. integrifolium Steetz in Seem., Bot. Voy. Herald 160. 185.

Small glabrate *herbs*; stems prostrate and ascending, to 20 cm long, sparingly branching, with a small tap root. *Leaves* oblanceolate, to 10 cm long and 2.5 cm wide, apically dentate and rounded to obtuse, mostly entire below, basally narrowed and the slender petiole not differentiated from the blade, slightly clasping the stem, pinnately veined mostly in the upper portion, often drying reticulate on both sides, glabrate, ?succulent. *Inflorescence* a solitary head; peduncle ascending, slender, glabrate, to 15 cm long, sometimes minutely

FIGURE 80. *Chrysanthellum americanum* var. *integrifolium* (Steetz) Alexander.—A. Habit (× ⅘).—B. Achenes (× 5). [After *Duke* 5933 (MO).]

puberulent at the apex, sometimes with one or two foliaceous or scalelike bracts along the length. *Heads* radiate; involucral bracts of 2 dissimilar forms, the outermost 4–8, subulate, ca. 2 mm long and 0.5 mm wide, apically acute, basally enlarged into a (?succulent) boss, the innermost 13–18 bracts in 2 similar series, imbricate, 3–5 mm long, 1.5 mm wide, oblong, apically obtuse, drying reddish brown, indurate, the margins broad, hyaline, entire; receptacle depressed-hemispherical; paleas linear, drying dark-striate, exceeding the ovaries but mostly shorter than the filaments, nearly flat; ray florets ca. 18 in 2–3 series, ca. 9 mm long, the corolla yellow, 6–7 mm long with two prominent, puberulent, brownish-red longitudinal stripes, apically 2(3)-denticulate, the tube ca. 1 mm long, the style branches flattened, glabrous, the style with 2 vascular traces, basally minutely

expanded, the ovary narrowly turbinate, laterally flattened, pubescent with weak, multicellular hairs, half enfolded by palealike bracts; disc florets ca. 13, ca. 4 mm long, the corolla campanulate with a short tube and 5 glabrous lobes, the lobes veinless, the anthers dark, 1 mm long, the appendages clear, deltoid, the style branches flattened, pilose ventrally and marginally, the style with 2 vascular traces, not basally expanded, the ovary oblong, compressed. *Achene* oblong, strongly flattened, 3 mm long, 1–2 mm wide, black with massive, light-colored wings; pappus wanting.

Chrysanthellum americanum grows in wet, sunny spots in lowland Panama. The wings of the achenes are larger and more massive relative to the flat, black central portion than in any other epappose species of Compositae in Panama.

Variety *integrifolium* has entire or apically dentate leaves, while the typical var. *americanum* has dissected leaves with filiform segments. The heads of var. *integrifolium* are larger as well. Variety *integrifolium* is reported to have only one sort of achene, but this may not be true of all plants. Both varieties occur on Jamaica, the type locality for the species. The typical variety ranges across the Old and New World tropics, but var. *integrifolium* appears to be restricted to the Caribbean region.

CANAL ZONE: Fort Kobbe, *Duke* 3973 (MO). COCLÉ: Llanos, Penonomé, *Ebinger* 1028 (MO). Between Aguadulce and Antón, 15–50 m, *Woodson et al.* 1220 (MO). HERRERA: Pesé, ca. 50 m, *Allen* 811 (MO). PANAMÁ: Savanna near Río Pacora and Chepo Hwy., *Duke* 5933 (MO). Sabana de Juan Corso near Chepo, 60–80 m, *Pittier* 4505 (MO).

79. COSMOS

Cosmos Cav., Icon. Descr. Pl. 1: 9. 1791. TYPE: *C. bipinnatus* Cav.

Cosmea Willd., Sp. Pl., ed. 4. 3: 2250. 1803, orth. mut. *Cosmos* Cav.
Cosmus Pers., Syn. Pl. 2: 477. 1807, orth. mut. *Cosmos* Cav.
Adenolepsis Less., Linnaea 6: 510. 1831. TYPE: *A. pulchella* Less.

Herbs or rarely *subshrubs*, perennial or annual, mostly glabrate, sometimes hispid; stems branched, erect, slender, quadrate or terete; roots of perennial species thickened, fasciculate. *Leaves* opposite, mostly compound or dissected, petiolate. *Inflorescence* a solitary head or loose aggregate of heads; peduncles elongate, terete or slightly angled; bracts resembling the leaves, one or two bracteoles sometimes alternate along the peduncle. *Head* normally radiate, sometimes showy; involucral bracts in 2 dissimilar series each about as many as the ray florets, the outermost herbaceous, drying striate, basally fused into a meniscoid hypanthium, the innermost longer, broader, membranous, mostly not striate, sometimes colored like the rays; receptacle nearly flat; paleas scarious-membranous, flat or cuculate, curved around the ovary; ray florets 5–12 in 1 series (except some horticulture forms), the corolla variously colored, the limb 3-denticulate, longitudinally sulcate with scattered elongate slender hairs on the dorsal surface, the ventral surface minutely puberulent-papillose near the base, the tube short, dorsiventrally compressed, the ovary rudimentary; disc florets few–many, often forming a cone or cylindrical disc, colored like the rays or not, the corolla cylindrical or narrowly obconical, the limb not demarcated from the tube, faintly 5-angled, glabrate,

5-lobed, the lobes obtuse, ciliate or ventrally pubescent, the point of filament insertion marked by a ridge on the corolla tube, the anthers with large appendages, basally obtuse or subauriculate, the filaments pubescent, the style branches pilose, truncate with a short or long acicular appendage, often appearing acicular overall, the ovary subcylindrical, with the basal half slightly enlarged, sometimes strigose. *Achenes* narrowly cylindrical-fusiform, often apically narrowed into a slender beak, sometimes strigose, mostly with 1–3 stout, barbed awns.

Cosmos includes about 30 species occurring mainly in Mexico but ranging south into Central America. It is closely related to *Dahlia*, *Coreopsis*, and *Bidens*. *Dahlia* is distinguished by its naked awns and more robust habit. *Coreopsis* does not have thickened rootstocks and the awns are not barbed. In *Bidens* the achene apex is not produced into a distinct beak.

Three easily distinguished species of *Cosmos* occur in Panama. One of these, *C. sulphureus* is known mainly from cultivation. *Cosmos bipinnatus* Cav., native of Mexico and Arizona, is frequently cultivated for ornament in other countries and may be expected in Panamanian gardens from imported seed. It resembles *C. crithmifolius* but is annual instead of perennial, and the similar leaves are shorter and softly flexuous instead of stiffly erect. *Cosmos bipinnatus* is available from northern seed houses in various colors.

a. Leaf segments stiff, uniform in width (1–2 mm); perennial; rays showy pink; bristles at summit of achene 1–5 and erect ..... 2. *C. crithmifolius*
aa. Leaf segments membranaceous, flexuous, conspicuously wider (to 6 mm) near the middle; annual; rays various colors; bristles at summit of achene 0–3, divaricate, seldom erect.
  b. Flowers showy yellow; anthers yellow; inner involucral bracts mostly orange or yellowish at the tips; cultivated species sometimes escaping ..... 3. *C. sulphureus*
  bb. Flowers pink or purplish (?or white), mostly not showy; anthers black; inner involucral bracts mostly not colored; native species ..... 1. *C. caudatus*

1. **Cosmos caudatus** H.B.K., Nov. Gen. Sp. Pl. 4: 240. 1820. TYPE: Mexico, *Humboldt & Bonpland* (P).

Erect, annual *herb* to 2 m tall; stems slender, terete, glabrate with occasional sturdy hairs, drying striate. *Leaves* to 20 cm long, 2–3-pinnatisect, the segments to 6 mm broad, apically acute, aristate; petiole slender, to 8 cm long but shorter or wanting on the uppermost leaves, the margins basally hirsute. *Inflorescences* of 1–3 heads in an open cluster; peduncle slender, elongate, subtended by bracts resembling reduced leaves, sometimes bearing one or more alternate, scalelike bracteoles. *Heads* radiate, rarely showy; involucral bracts in 2 unlike series, the outer series ca. 8, herbaceous, slender, ca. 7 mm long, the midvein basally prominent on drying, the inner series scarious, longer and broader, colored with hyaline margins; paleas resembling the innermost bracts but narrower and lacking color; ray florets mostly pink or purplish, 10–15 mm long, sometimes abortive, the limb apically entire or 2–3-denticulate with scattered long hairs on the dorsal surface and minutely puberulent near the base on the ventral surface; disc florets numerous, the corollas yellowish tipped, 5–6 mm long, cylindrical but expanding slightly upwards, the lobes copiously pubescent ventrally, the anthers black, ca. 2 mm long, the appendages hyaline, costate with a projection of the anther con-

nective, the bases obtuse or subauriculate, the filaments inserted about ⅓ of the way up the corolla tube, puberulent, the style branches pilose, yellow, with short, acicular appendages, inserted on a 0.6 mm long, narrow, cylindrical nectary, the ovary as long as the corolla, fusiform, larger in the lower half, curved. *Achene* mostly black, 1–3 cm long, fusiform, compressed, sulcate, slightly curved, the upper ⅓ produced into a brown, ascending-strigose beak terminated by 2 diverging, retrorsely strigose, 3–4 mm long bristles.

Cosmos caudatus is native to Central America and the Antilles but is now widespread in many parts of the world. It has probably been distributed adventively as a weed but may occasionally be cultivated for ornament. It is not usually a showy bloomer. With leaves much like those of *C. sulphureus*, *C. caudatus* is distinguished by its smaller pinkish rays, larger achenes, and less pubescent filaments which are inserted higher in the corolla tube. "Pega pega," Clavijena de Monte."

BOCAS DEL TORO: Changuinola to 5 mi S at junction of Río Changuinola and Terebé, 100–200 ft, *Lewis et al. 906* (MO). CANAL ZONE: Between Mount Hope and Santa Maria Trail, *Cowell 91* (NY). Banks of Gatún River, *Greenman & Greenman 5151* (MO). Ancón Hill, *Paul 156* (US). Empire to Mandinga, *Piper 5531* (US). Around Culebra, *Pittier 2152* (US). Between Gorgona and Mamei, *Pittier 2246* (US). Between Fort Clayton and Corozal, *Standley 29029* (US). Near Fort Sherman, *Standley 31069* (US). COCLÉ: El Valle de Antón, 1000–2000 ft, *Lewis et al. 2574* (MO). 1–5 mi S of Antón, *Tyson & Blum 2584* (MO). COLÓN: Between France Field and Cativa1, *Standley 30409* (US). DARIÉN: 10 mi S of El Real on Río Pirre, *Duke 5377* (MO). HERRERA: Between Las Minas and Pesé, 900–1200 ft, *Burch et al. 1350* (MO). 10 mi S of Ocú, *Tyson & Blum 2869* (MO). PANAMÁ: Nueva Gorgona, *Duke 4489* (MO). Near El Llano, *Duke 5515* (MO). Tocumen, *Dwyer 5161* (MO). Chiva-Chiva, *Killip 3134* (US). Between Las Sabanas and Aguarubia, *Killip 3354* (GH). Between Savannas and Yguana, *McBride 2656* (F, US). Without locality, *Seeman* (GH). Past Río Mamoní 3 mi along road to El Llano, *Tyson 6797* (MO). SAN BLAS: Outskirts of Puerto Obaldía, *Gentry 1566* (MO). Mainland opposite Ailigandí from mouth of Ailigandí River, 2.5 mi inland, *Lewis et al. 79* (MO). VERAGUAS: 4 mi N of Santiago, *Dwyer 1245A* (MO). WITHOUT LOCALITY *Duke 6163* (MO).

2. **Cosmos crithmifolius** H.B.K., Nov. Gen. Sp. Pl. 4: 242. 1820. TYPE: Mexico, *Bonpland* (P).—FIG. 81.

Erect, branched perennial *herb*, sometimes woody near the base, to 1 m tall; stems slender, green, glabrate, the angles conspicuously lighter in color. *Leaves* to 10 mm long, pinnate, the segments and petiole linear, evenly 1–2 mm wide, the midvein conspicuous on both sides. *Inflorescence* of 1–4 heads at a terminal node; peduncle slender, angled, to 20 mm long, sometimes with 1 or 2 alternate or opposite, scalelike bractlets along their length. *Heads* radiate, showy; outer involucral bracts narrow, herbaceous, drying with the veins elevated, 4–8 mm long, the inner bracts almost twice as long, hyaline, broad, colored or not; ray florets ca. 5, bright pink, the limb broad, apically 3-dentate, conspicuously longitudinally sulcate or nerved with scattered, long white hairs near the base on

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FIGURE 81. *Cosmos crithmifolius* H.B.K.—A. Habit (× ⅗).—B. Achene (× 3⅘). [After *D'Arcy & D'Arcy 6461* (MO).]

B
A
JLW
M.E. WILSON

the dorsal surface, the tube 2–3 mm long; disc florets numerous, the corolla yellowish or pinkish, cylindrical, ca. 10 mm long, the lobes dorsally puberulent, the anthers black, the appendages ca. 0.8 mm long, the style branches compressed, ?glandular, the apex and the caudex pilose. *Achene* brown, ascending-strigulose, with 1–5 stiff, erect, retrorsely strigose awns.

Cosmos crithmifolius is native from southern Mexico to Honduras, and the Panamanian collection represents a significant range extension. It is an upland species of open woods. Similar to *C. bipinnatus* Cav. which may be cultivated from time to time in Panama, this species differs in its stiff leaves with segments 1–2 mm wide. *Cosmos bipinnatus* has weak leaves, and the segments are mostly 1 mm wide or less. It often has much longer outer involucral bracts as well.

CHIRIQUÍ: N end of Boquete, 4000 ft, *D'Arcy & D'Arcy 6461* (MO).

3. **Cosmos sulphureus** Cav., Icon. Descr. Pl. 1: 56. 1791. TYPE: not seen.

C. gracilis Sherff, Bot. Gaz. (Crawfordsville) 88: 304. 1929. TYPE: Panama, *Pittier 5053* (US).

Annual *herb* to 1 m tall; stems slender, branching, erect, slightly quadrate, glabrate but with a few scattered, large whitish hairs. *Leaves* to 15 cm long, 2- or 3-pinnatisect, the segments acuminate and aristate-tipped, to 3–5 mm broad, glabrous or with a few stout hairs; petiole slender, angled, much shorter or wanting in the upper leaves, often hispid-ciliate at the expanded base. *Inflorescences* of one or more heads arising at terminal nodes; peduncles slender, to 15 cm long, apically narrowed, one or more leaflike bracts sometimes alternate along its length. *Heads* radiate, showy orange, to 5 cm across; outer involucral bracts ca. 8, herbaceous, slender, 5–7 mm long, drying basally striate, the inner bracts membranous-scarious, broader and longer than the outer bracts, drying without striations; paleas resembling the innermost involucral bracts but narrower, partly enfolding the floret; ray florets ca. 8 (a second series present in some horticultural forms), the corolla yellow or orange, 15–20 mm long, the limb obovate, apically 3-denticulate, longitudinally sulcate, sparingly pilose dorsally, minutely papillose-puberulent basally on the ventral surface, the tube 1–2 mm long, the ovary rudimentary; disc florets numerous forming a cylindrical, apically rounded disc, the corollas cylindrical, 7–12 mm long, the tube not demarcated from the limb, the apical lobes narrowly obtuse, ciliate on the inner surface, the anthers yellow, ca. 3 mm long, the bases acute or sometimes subauriculate, the filaments inserted near the bottom of the corolla tube, flattened, densely ciliate, the style branches yellow, pilose, the appendix slender, elongate, the ovary cylindriform, slightly expanded basally, the angles with short ascending hairs. *Achenes* black, ca. 20 mm long, slender, slightly curved, sharply angled, somewhat compressed, the upper ⅓ narrowed into a linear, ascending-strigose beak terminated by 2 porrect, retrorsely strigose bristles 3 mm long.

A native of Mexico and Guatemala, this species is widely cultivated for ornament and is known from escapes and naturalized populations in many other parts of the world including Panama. It is usually recognized at a glance by its showy yellow or orange flowers, slender stems, and dissected leaves. Throughout

its range, isolated plants or populations may have awnless achenes, and two of the collections cited below represent this condition (*Pittier 5053* and *Seibert 544*). Sherff considered this form to be a distinct species, *Cosmos gracilis*, but it is not worthy of taxonomic recognition. "Niño Muerto."

CANAL ZONE: Hotel Washington, Cristóbal, *Bailey & Bailey 692* (US). Fort Kobbe, *Duke 3949* (MO). Chagres, *Fendler 173* (US). Río Pedro Miguel near East Paraíso, *Standley 30005* (US). COCLÉ: 10 mi E of Río Hato, *D'Arcy & D'Arcy 6274* (MO). Near Olá, *Pittier 5053* (GH, US). Llano Bonito N of Las Margaritas, 400–500 m, *Seibert 544* (MO, US). PANAMÁ: Panama City, *Hunter* 18 Dec 1934 (NY, GH).

80. DAHLIA

Dahlia Cav., Icon. Descr. Pl. 1: 56. 1791. TYPE: *D. pinnata* Cav.

Georgina Willd., Sp. Pl., ed. 4. 3(3): 2142. 1803. TYPE: *G. purpurea* Willd. = *Dahlia pinnata* Cav.

Georgia Spreng., Anleit., ed. 2. 2: 567. 1818, orth. mut. *Georgina* Willd.

Mostly perennial *herbs*, sometimes shrubby, rarely (?hemi-)*epiphytes*; stems branched or not, sometimes fistulose; mostly with thickened rootstocks. *Leaves* opposite or 3 per node, simple or pinnately 1–3-compound, the leaflets ovate to linear, the margins mostly serrate or dentate; stipels and petioles present. *Inflorescence* a solitary terminal head; peduncles sometimes aggregated into corymbs of panicles. *Heads* radiate, sometimes large and showy; involucral bracts in 2 unlike series, the outer series 4–7, green, porrect or reflexed, linear to ovate, somewhat fleshy, longitudinally striate-nervate, the inner series 7–9, thinner, broader, sometimes scarious margined, imbricate, accrescent in fruit; paleas scarious or slightly indurate; ray florets numerous, showy, variously colored, the limb broad or narrow, often apically denticulate, sometimes dorsally puberulent, the ovary sterile; disc florets numerous, much shorter than the rays, the corolla yellow or with some reddish or purplish, tubular, apically 5-lobed, the anthers with deltoid apical appendages and obtuse bases, the style branches narrow, dorsally pilose and ventrally puberulent at the tips. *Achene* mostly linear, apically contracted, surmounted by a thickened cap; pappus wanting or of 2 rudimentary awns or threads.

A genus of about two dozen species, *Dahlia* is mostly Mexican but ranges south into Colombia. Two species, *D. pinnata* Cav. and *D. coccinea* Cav. have hybridized in cultivation to produce the majority of horticultural forms commonly grown for ornament in many parts of the world.

Literature:

Sorenson, P. D. 1969. Revision of the genus *Dahlia* (Compositae, Heliantheae-Coreopsidinae). Rhodora 71: 309–416.

a. Herb or shrub to 4 m tall; leaflets opposite, pubescent on the veins on both sides; inner involucral bracts twice as long as the outer bracts; ray florets white or pale pink, violet or purple, the disc prominent and yellow ..... 1. *D. imperialis*

aa. Herb to 1.5 m tall; leaflets randomly placed on the rachis, glabrate; inner involucral bracts slightly longer than the outer bracts; ray florets variously colored, the disc prominent or not, sometimes absent, yellow or purplish ..... 2. *D. pinnata*

1. **Dahlia imperialis** Roezl ex Ortgies, Gartenflora 12: 243. 1863. TYPE: Mexico, *Roezl* (B, if extant, not seen).—FIG. 82.

Perennial *herb* or *shrub*, rarely a tree to 4 m, mostly branched from the base; stems stout; rootstock not seen. *Leaves* opposite, 35 cm or longer, 1–3-pinnate, the leaflets ovate, apically acuminate, basally rounded or obtuse, the margins evenly serrate, appressed puberulent on the veins above, loosely pilose beneath, especially on the veins, reticulate veined beneath; petiole stout, slightly shorter than the laminate portion. *Inflorescence* a terminal, several-flowered panicle, the branches subtended by foliaceous bracts and reduced leaves resembling abortive peduncles; peduncle glabrous, stout, of varying length, tardily articulating near the apex. *Heads* large, radiate; involucral bracts in 2 unlike series, the outermost oblong, thickened, reflexed, ca. 10 mm long, the innermost twice as long, broadly ovate, scarious, drying dark brown with hyaline margins; ray florets ca. 9, the corollas white or lavender, the ligule narrowly elliptical or oblanceolate, 2–4 mm long; disc florets very numerous, yellow. *Achene* (Sorenson) 13–17 mm long, linear or slightly oblanceolate.

This species was previously reported (Sorenson, 1969) from Mexico to Costa Rica and from Colombia on the east. The Panamanian collection reported here removes the disjunction between northern and southern populations. The species is sometimes cultivated for ornament in other countries and the possibility that the Panamanian collection represents a feral element cannot be discounted.

Dahlia imperialis differs from the commonly cultivated *D. pinnata* in its large size, its woody perennial growth, and in other characters noted in the key.

CHIRIQUÍ: 2 mi SW of Cerro Punta, 5600 ft, *Tyson 6352* (MO).

2. **Dahlia pinnata**[54] Cav., Icon. Descr. Pl. 1: 57. 1791. TYPE: not seen.

Erect, sometimes branched, cultivated *herbs* to 1.5 m tall; stems stout, sparingly branched, glabrous or scabridulous with sparse hairs, often reddish or purplish; rootstock not seen. *Leaves* opposite, simple or 1–2-pinnate, the leaflets ovate or elliptical, apically acuminate, basally obtuse or acute, the margins serrate or remotely dentate, to 15 cm long, glabrate, the petiolules mostly short, the petiole slender or stout, sometimes partly winged, basally expanded and with an intrapetiolar ridge. *Inflorescence* mostly a solitary terminal nodding head on an elongate, naked peduncle but sometimes several clustered into a pseudopanicle. *Heads* radiate, large, to 15 cm across; involucral bracts in 2 dissimilar series, the outermost ca. 10 mm long, oblong, apically obtuse or acute, patent, thick, many nerved, the innermost slightly longer, narrower, thin, drying dark and scarious, sometimes with a scarious margin; ray florets showy, extremely variable, purple, red, or white (rarely yellowish), ovate to linear, to 5 cm long, the ovary sterile; disc florets mostly yellow but sometimes reddish or purplish, sometimes replaced by fertile or sterile ligulate florets. *Achene* not seen.

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[54] For a list of synonyms see Sorensen (1969).

FIGURE 82. *Dahlia imperialis* Roezl ex Ortgies.—A. Leaf (× ½).—B. Head, top view (× ½).—C. Head, bottom view, the corollas removed (× ½). [After *Tyson* 6352 (MO).]

The cultivated *Dahlia* is grown in many countries and exhibits wide variation in form of the flowers. It is best recognized by the large heads and by the two series of involucral bracts, the outermost of which is fleshy, patent or reflexed and the innermost is thin, seldom drying green yet not quite indurate. In Panama the species is grown in the Chiriquí mountains from imported seed, and it makes its appearance as cut flowers in lowland markets.

Sorensen (1969) discussed the uncertain origin of what is today grown as *Dahlia pinnata*, and he recommended against use of this name for the wide range of material in cultivation. Use of cultivar names as he suggested will be satisfactory only for horticultural purposes. Under the International Code of Botanical Nomenclature, the name *Dahlia pinnata* is currently the best choice, although it must be understood to include considerable variability derived from hybridization with other species. Selection of another, later, name from Sorensen's synonymy to express the advanced hybrid nature of plants now in cultivation is desirable, but must be made with reference to the appropriate types.

CHIRIQUÍ: Cultivated in Boquete, *D'Arcy & D'Arcy 6465, 6509* (both MO).

81. HIDALGOA

Hidalgoa LaLlave & Lexarza, Nov. Veg. Descr. 1: 15. 1824. TYPE: *H. ternata* LaLlave.

Vines climbing by hooked petiole bases; stems weak, slender, sulcate, puberulent, sometimes woody at the base. *Leaves* opposite, trifoliolate, 1–2-pinnate or palmately compound, the leaflets lobed or serrate; petioles mostly elongate and slender, the basal portion often lignified, recurved and following detachment of the apical portion, becoming a stout hook. *Inflorescences* axillary, mostly few or solitary along the stem; leaflike or scalelike bracts mostly present; scalelike bracteoles occurring sometimes along the petiole. *Heads* radiate, sometimes showy; involucral bracts in 2 dissimilar series, the outer series ca. 5, linear, porrect, the inner series broad, membranaceous, imbricate; ray florets 5–8, the corolla variously colored, apically minutely denticulate, drying prominently longitudinally nerved, the ovary dorsiventrally flattened, rectangular, surmounted by 2 stout, hornlike processes; disc florets numerous, the corolla tubular, long exserted from the paleas, 5-lobed, glabrous, the anthers basally obtuse or subauriculate, the appendages short, the style long exserted, branched or not, granular, the ovary sterile. *Achenes* (after Sherff) obcompressed, elongate-linear, mostly biaristate.

Hidalgoa includes 4 species which range from Mexico (Vera Cruz) to Peru. The plants are apparently rarely collected members of the liana-canopy accompaniment of forests. Only one species occurs in Panama.

The genus superficially resembles *Bidens* but differs markedly in a number of features, e.g., the hooked, lignified petiole bases, the porrect outer involucral bracts, the flat, rectangular ovaries of the ray florets and the abortive ovaries of the disc florets. The heads apparently appear in many colors. To judge from the shape of the achenes, the genus is related to *Bidens*, particularly such species as *B. vulgata* E. L. Greene of Canada and the northeastern United States.

FIGURE 83. *Hidalgoa ternata* LaLlave & Lexarza.—A. Habit (× ⅖).—B. Achene (× 4). [After *Liesner* 857 (MO).]

1. **Hidalgoa ternata** LaLlave & Lexarza, Nov. Veg. Descr. 1: 15. 1824. TYPE: Mexico, *LaLlave* (not seen).—FIG. 83.

Slender *vine*, climbing by hooked petioles; stems puberulent, weak, drying sulcate, the nodes somewhat enlarged. *Leaves* opposite, trifoliolate, the leaflets 3–4 cm long, ovate, apically acuminate, basally narrowed, irregularly serrate, the venation pinnate with 4–8 lateral veins on each side of the midvein, glabrate; petiolules short or wanting; petiole slender, weak, to 8 mm long, the basal 5–8 mm on some leaves becoming lignified, curved and hooklike, the distal portion deciduous. *Inflorescence* of solitary or paired heads distributed along the stem; peduncles slender, weak, sulcate, to 7 cm long, subtended by 1–2 entire bracts, sometimes with a bracteole along the length. *Heads* radiate; involucral bracts in 2 dissimilar series, the outermost ca. 5, linear, porrect, 8–14 mm long, herbaceous, thick, the midvein prominent, the inner series membranous, ca. 7 mm long and 3 mm wide, drying striate, the margins lighter in color; paleas resembling the inner involucral bracts but narrower; ray florets ca. 5, the corolla yellow, orange, red, or pink, 7–20 mm long, apically denticulate, the numerous longitudinal veins conspicuous, the ovary dorsiventrally flattened, rectangular, apically indented between the 2 hornlike lobes, pappus of a minute retrorsely barbed awn on each lobe, or wanting; disc florets numerous, the corolla tubular, slightly curved, ca. 8 mm long, long-exserted from the palea, glabrous outside, the lobes 1 mm long, glabrous, the anthers dark, 2 mm long, basally obtuse or auriculate, the apical appendages short, emarginate, the filaments glabrous, the style branches united, long-exserted, the surface granular, the ovary sterile. *Achene* (after Sherff) blackish, 7–11 mm long, ca. 4 mm wide, apically 2-dentate, slightly winged, papillose in rows, strigose.

Hidalgoa ternata ranges from Mexico (Vera Cruz) to Peru, but has been collected in Panama infrequently. It is usually found climbing at the edge of forests.

This species may be recognized by its scandent habit and hooked petiole bases which apparently assist in climbing. The heads are subtended by narrow, porrect outer involucral bracts.

VERAGUAS: Río Primero Braso, 2.5 km beyond Agricultural School Alto Piedra near Santa Fe, 700–750 m, *Croat 25505* (MO). 5 mi SW of Santa Fe on road past Escuela Agrícola de Alto Piedra on Pacific side of the divide, 800–1200 m, *Liesner 857* (MO). N of Santa Fe on property of Escuela Agrícola de Piedra, *Mori & Kallunki 2513* (MO).

82. SYNEDRELLA

Synedrella Gaertn., Fruct. 2: 456, *tab. 171, fig. 7.* 1791, nom. cons. TYPE: *S. nodiflora* (L.) Gaertn.

Ucacou, Adanson, Fam. 2: 615. 1763. LECTOTYPE: *U. nodiflorum* (L.) Hitchc.
Ukakou, Adanson, Fam. 2: 615. 1763, nom. nud.
Ucacea, Cass., Dict. Sci. Nat. 29: 489. 1823. Revised spelling of *Ukakou* Adanson.

Branching *herb*, erect or procumbent. *Leaves* opposite, chartaceous, serrate, pubescent with appressed white hairs; petiole winged, short. *Inflorescences* fascicles of heads in the leaf axils; peduncles short, sometimes with foliaceous bracts. *Heads* radiate, cylindrical; involucral bracts several, imbricate, the outermost green, those inward scarious, narrower; receptacle convex, minute; ray florets 4–5, the corolla yellow with a substantial, narrow tube and broad limb, apically denticulate, the style branches slender, pilose, the ovary dorsiventrally flattened, with broad, apically erose margins, 2 awns evident; disc florets several, the corolla tube nearly as long as the angled, obconical limb, the short lobes dorsally pubescent, the anthers dark, the appendages dark, ligulelike, the basal auricles rounded, the style branches slender, flattened, marginally pilose, the style base not expanded but inserted in a slender, elongate, apically erose, stipitate nectary, the ovary oblong, slender, with 2 apical awns and a thick cap. *Achenes* dimorphic, those of the ray florets flat with broad, light colored, toothed margins and 2 short apical awns, those of the disc florets slender, tuberculate, with 2 sturdy, diverging strigose awns.

A monotypic genus ranging through the tropics, *Synedrella* may be recognized by its fascicles of inconspicuous heads and by the two distinct types of achenes.

1. **Synedrella nodiflora** (L.) Gaertn., Fruct. 2: 456. 1791.—FIG. 84.

Verbesina nodiflora L., Cent. I. Pl. 28. 1755. TYPE: not seen.
Ucacau nodiflorum (L.) Hitchc., Annual Rep. Missouri Bot. Gard. 4: 100. 1893.

Herb to 1.5 m tall, dichotomously branching, erect, sprawling or sometimes procumbent; stems terete, puberulent with appressed, ascending white hairs; sometimes rooting along the stem without respect to the nodes. *Leaves* opposite, mostly at the stem dichotomies, mostly 3–10 cm long, ovate or elliptical, apically acuminate, basally obtuse, the margins callose-serrate to subentire, both sides with appressed ascending white hairs, rarely scabridulous, the veins appearing pinnate

B

C

A

FIGURE 84. *Synedrella nodiflora* (L.) Gaertn.—A. Habit (× ½).—B. Outer Achene (× 6⅗).—C. Inner achene (× 6⅗). [After *Croat 8162* (MO).]

or 3-nerved from near the base; petiole short, 5–10 mm long, winged, the margin and keel ciliate. *Inflorescence* a fascicle of 1–many heads at a dichotomy of the stem or leaf axil, the heads aggregated in groups of 1–4; peduncles to 2 mm long, stout; foliaceous bracts sometimes present. *Heads*, radiate, cylindrical, ca. 8 mm long and 5 mm thick; involucral bracts several, imbricate, oblong, apically acute, obtuse or erose, the outermost green, nervate, becoming stramineous, narrower

and scarious inwards; receptacle convex; ray florets 4–5, ca. 6 mm long, the corolla yellow, 3–4 mm long, glabrous, the tube 1.5–2 mm long, apically notched or denticulate with 2 main veins, the limb broad, the style branches flattened, slender, pubescent, the style base not enlarged, the ovary dorsiventrally flattened, oblong, apically erose, the erose margins partly obscuring the two strigose awns; disc florets several, ca. 8 mm long, the corolla yellow, 3 mm long, the tube narrow, forming about one half the length, the limb narrowly obconical, angled, the lobes short-deltoid, dorsally pubescent, the anthers dark, the appendages large, the basal auricles rounded, the style branches flattened, marginally pilose, the style base not expanded but inserted in a narrow, stipitate, ca. 1 mm long, apically fimbriate or sinuate nectary, the ovary slightly compressed, oblong, with 2 flattened, stout, apical awns and a connecting ring of hairs or erose scales. *Achenes* dimorphic, those of the ray florets 3–5 mm long, ovate, flattened, the body black with a 1 mm broad, winglike margin bearing short ascending awns similar to the apical pair of true awns, those of the disc florets with a black, ca. 3 mm long, slender, tuberculate body; pappus a pair of stout slender, strigose awns.

This is a common species of disturbed areas in lowland Panama occurring in towns, fields, and roadsides.

BOCAS DEL TORO: Almirante, *Blum 1324* (MO). Changuinola, *Carleton 49* (GH). Changuinola to 5 mi S at junction of Río Changuinola and Terebé, *Dwyer et al. 916* (GH, MO); *Lewis et al. 2072* (GH, MO, US). Water Valley, Chiriquí Lagoon, *Wedel 768* (GH); *1677* (MO). Isla Colón, *Wedel 2851* (GH, MO, US). CANAL ZONE: Fort San Lorenzo, *Burch et al. 1045* (GH, MO). Madden Forest Road, *Croat 8932* (MO). Pipeline Road at Río Frijoles, *Croat 12338* (MO). Fort Kobbe, *Duke 3916* (MO). Navy Corrosion Laboratory, *Duke 4437* (MO). U.S. Army Tropic Test Mine Emplacement, *Dwyer 8537* (MO). Ancón, *Greenman & Greenman 5007* (MO). Government forest along Las Cruces Trail, *Hunter & Allen 744* (MO). 2 mi N of road to Fort Sherman, *Lazor & Blum 5429* (MO). Near Culebra, *Pittier 2102, 4065* (both GH). Chiva Chiva trail to Pueblo, *Piper 5712* (US). Along Corozal Road, *Standley 26830* (US). Near Fort Randolph, *Standley 28956* (US). Fort San Lorenzo, *Tyson & Blum 3700* (MO). 12 mi S of Colón on Río Providencia, *Tyson & Blum 3940* (MO). Curundú, *Tyson 4185* (MO); *6287* (MO). Across railroad from Summit Garden, *Tyson 6394* (MO). BARRO COLORADO ISLAND: *Croat 5909, 6961, 7389* (all MO), *8162* (MO, US); *Ebinger 592* (MO). CHIRIQUÍ: Puerto Armuelles, *Busey 504* (MO). Quebrada del Medio, 2 km N of Punta de Burica, 40–80 m, *Busey 764* (MO). 1.6 mi W of Puerto Armuelles, *Croat 21922* (MO). COCLÉ: El Valle de Antón, *Allen 4228* (MO). Near El Valle de Antón, *Croat 13282* (MO). COLÓN: Near Sardinilla, *Blum & Tyson 498* (MO). Peluca, ca. 27 km from Trans-isthmian Hwy. on road to Nombre de Dios, *Kennedy 2624* (MO). Near Peluca along Río Boquerón, *Kennedy 2810* (MO). DARIÉN: El Real, *Burch et al. 1077* (GH, MO, US). Río Sabana, 0–4 mi above Santa Fe, *Duke 4143* (GH, MO). HERRERA: 12 mi S of Ocú on Las Minas Road, *Graham 229* (GH). LOS SANTOS: Playa de La Concepción, *Burch et al. 1265* (GH, MO, US). PANAMÁ: Isla Taboga, *Allen 1300* (MO, US). Las Delicias, *Carleton 49* (GH). Tocumen, *Croat 9766* (MO). El Llano, near Río Bayano, *Gentry & Tyson 1716* (MO). Río Pasiga, *Gentry 2253, 2387* (both MO). Camino de las Sabanas, *Heriberto 189* (US). Cerro Campana on road to Su Lin, *Kennedy et al. 2031* (MO). 2 mi S of Goofy Lake, road to Cerro Jefe, *Lewis et al. 277* (GH). Taboga Island, *Macbride 2795* (US). Cerro Azul, 2000 ft, *Tyson 2061, 2193* (both MO). SAN BLAS: Near Puerto Obaldía, *Croat 16857, 16954* (both MO). VERAGUAS: 1 mi W of Santiago, *Tyson 5170* (MO).

83. TRICHOSPIRA

Trichospira H.B.K., Nov. Gen. Sp. Pl. 4: 27, *tab. 312.* 1820 (1818). TYPE: *T. menthoides* H.B.K. = *T. verticillata* (L.) Blake.

Small *herbs*, sprawling or erect. *Leaves* alternate, opposite in the inflorescence

region, spatulate, crenate or entire, glabrate above and tomentose beneath, sessile, sometimes with basal auricles. *Inflorescence* of heads sessile in the upper leaf axils. *Heads* small, discoid; corolla tubular, deeply lobed, 4–5-parted; anthers 4–5, the appendages small, the base sagittate; style pubescent upwards, the branches short, pubescent, nectary prominent. *Achene* dorsiventrally compressed, 2–3-ribbed on each side, the ribs and angles ciliolate; pappus of 2 strong diverging awns and several minute awns on the sides.

This is a monotypic genus of tropical America.

Literature:

Robinson, H. & R. D. Brettell. 1973. Tribal revisions in the Asteraceae II. The relationship of *Trichospira*. Phytologia 25: 259–261.

1. **Trichospira verticillata**[55] (L.) Blake, Torreya 15: 106. 1915.

Bidens verticillata L., Sp. Pl. 833. 1753. TYPE: not seen.
Trichospira menthoides H.B.K., Nov. Gen. Sp. Pl. 4: 28, *tab. 312*. 1820 (1818). TYPE: not seen.

Herbs, sprawling or erect, sometimes rooting at the lower nodes; branches tomentose, sometimes whitish, often drying sulcate. *Leaves* opposite in the inflorescence, alternate below, mostly spatulate, irregularly crenate, apically rounded, basally cuneate, discolorous, drying dark and glabrous above, the emerging leaves glandular punctate, beneath grey-tomentose with arachnoid hairs, the ca. 4 pinnate veins on each side of the midvein prominent; petiole wanting or consisting of a narrowed portion of the leaf blade, rotund, basal auricles often present. *Inflorescence* of single, paired heads axillary to the expanded and enveloping leaf bases. *Heads* discoid, 4–5 mm tall; involucral bracts 2–5, ca. 4 mm tall, oblong, hyaline, apically rounded and herbaceous, glabrous except on the tips; receptacle minute; paleas oblong, flat, hyaline with slightly expanded, pubescent, herbaceous tips; florets ca. 10, the corolla tubular, ca. 2 mm long, the 4 lobes oblong and forming ca. ½ the length, the anthers 4 with short, round appendages, the style apically pilose, the branches short, pilose, the nectary prominent. *Achenes* flat, cuneiform, 4–5 mm long, each side 2–3-ribbed, the ribs and angles minutely ciliate; pappus of 2 stout, diverging awns 1–2 mm long and several minute awns on each side.

This species occurs in muddy places at lower elevations. It may be recognized by its small discolorous leaves and flat, 2-awned achenes.

PANAMÁ: La Jagua, wet savanna area E of Panama City, *Bartlett & Lasser 16393* (MO).

G. GALINSOGINAE

JUDITH M. CANNE[56]

Galinsoginae Benth. in Benth. & Hook., Gen. Pl. 2: 217. 1873. TYPE: *Galinsoga* R. & P.

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[55] Other synonyms are presented by Blake but only the names noted here are pertinent to the Panamanian flora.

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84. CALEA

Calea L., Sp. Pl., ed. 2. 1179. 1763. TYPE: *C. jamaicensis* L.

Alloispermum Willd., Ges. Naturf. Freunde Berlin Mag. Neuesten Entdeck. Gesammten Naturk. 1: 139. 1807. TYPE: not designated.
Leontophthalmum Willd., Ges. Naturf. Freunde Berlin Mag. Neuesten Entdeck. Gesammten Naturk. 1: 140. 1807. TYPE: *L. peruvianum* H.B.K.
Calydermos Lag., Gen. Sp. Pl. Nov. 24. 1816. LECTOTYPE: *C. scaber* Lag., here chosen.
Mocinna Lag., Gen. Sp. Pl. Nov. 31. 1816. LECTOTYPE: *M. serrata* Lag.
Caleacte R. Brown, Trans. Linn. Soc. London 12: 109. 1818, nom. invalid.
Allocarpus H.B.K., Nov. Gen. Sp. Pl. 4: 291. 1820. TYPE: *A. caracasana* H.B.K.
Calebrachys Cass., Dict. Sci. Nat. 55: 265. 1828. TYPE: *C. pedunculares* (H.B.K.) Cass. ex Less.
Lemmatium DC., Prodr. 5: 669. 1836. TYPE: *L. rotundifolium* (Less.) DC.
Meyeria DC., Prodr. 5: 670. 1836. TYPE: not designated.
Tetrachyron Schlecter, Linnaea 19: 744. 1847. TYPE: *T. manicatum* Schlecter.
Stenophyllum Schultz-Bip. ex Benth. & Hook. f., Gen. Pl. 2: 391. 1873, pro syn.
Tonalanthus Brandegee, Univ. Calif. Publ. Bot. 6: 75. 1914. TYPE: *T. aurantiacus* Brandegee.

Perennial *herbs* or *shrubs*; stems glabrous to tomentose. *Leaves* opposite, petiolate or sessile; blades linear to ovate, with 1, 3 or 5 principal veins, margins entire, toothed, crenate, dentate or pinnatifid, surfaces glabrous to tomentose, often resin-dotted. *Inflorescences* of solitary heads or of heads in few- to many-headed cymose, corymbose, or umbellate clusters; peduncles axillary or terminal, to ca. 40 cm long, glabrous or pubescent. *Heads* variable in size, radiate or discoid, ovoid to cylindrical or campanulate; involucral bracts 3–many-seriate, imbricate, graduate, the outer bracts shorter and broader, scarious or the outer bracts herbaceous or herbaceous-tipped, glabrous or pubescent, flattened or convex; receptacle conical to flat; paleas scarious, white or pale yellow, flat to conduplicate, obtuse to aristate at the apex; ray florets fertile, one to several, the ligules white, yellow or roseate, ovate to oblong, entire or denticulate; disc florets fertile, the corollas white, yellow or orange with the limb cylindrical to campanulate, 5-lobed, the tube often flaring at the base, the anthers exserted, yellow or black, appendaged, basally sagittate. *Achenes* narrowly turbinate, subterete to 4–5-angled, glabrous to pubescent, black or reddish black; carpopodium present; pappus of a few to many setose bristles or blunt to aristate broad scales or absent. Chromosome numbers $x = 16, 18, 19$ (Powell & King, 1969).

Calea is a genus of nearly 100 species, sorely in need of taxonomic revision. The genus ranges from Mexico through Central America into South America.

Literature:

Powell, A. M. & R. M. King. 1969. Chromosome numbers in the Compositae: Colombian species. Amer. Jour. Bot. 56: 116–121.
Robinson, B. L. & J. M. Greenman. 1896. Revision of the Mexican and Central American species of the genus *Calea*. Proc. Amer. Acad. Arts 32: 20–30.
———. 1899. Supplementary notes upon *Calea*, *Tridax*, and *Mikania*. Proc. Boston Soc. Nat. Hist. 29: 105–108.

a. Heads radiate ..... 3. *C. urticifolia*
aa. Heads discoid.
b. Outer involucral bracts oblong to narrowly ovate, 1–3 mm long, 0.6–1.5 mm wide ..... 1. *C. pittieri*
bb. Outer involucral bracts ovate-oblong to rotund, 0.6–3.6 mm long, 1–6 mm wide ..... 2. *C. prunifolia*

1. **Calea pittieri** B. L. Robinson & Greenman, Proc. Boston Soc. Nat. Hist. 29: 105–106. 1899. SYNTYPES: Costa Rica, banks of the Río Ceibo near Buenos Aires, 200 m, Jan. 1892, *Pittier 4913* (GH, not seen). Costa Rica, chemin de Caldera between San Mateo and San Ramón, *Biolley 7015* (US).—FIG. 85C.

Shrub 1–3 m tall; stems terete to angular on younger branches, rusty brown, puberulent to tomentose. *Leaves* opposite; blades ovate to elliptic, apically acute, basally short attenuate to rounded, the margins crenate-serrate, 1.4–6.8 cm long, 0.7–4.5 cm wide, both surfaces rugose, upper surface green and scabrous, prominently 5-veined, lower surface resin-dotted, pale and tomentose; petioles 0.3–1.3 cm long, tomentose. *Inflorescences* hemispherical, umbellate clusters of heads on the ends of branches; peduncles slender, brown, 0.4–1.8(–2.9) cm long, tomentose to hirsute, occasionally resin-dotted. *Heads* discoid, campanulate, 3–9 mm wide, 5–13 mm tall; involucral bracts multiseriate, the outermost bracts herbaceous, oblong to narrowly ovate, tomentose to hirtellous, 1–3 mm long, 0.6–1.5 mm wide, the intermediate bracts scarious with erose, rounded, brownish tips, somewhat squarrose, the inner bracts lance-oblong, shiny yellow, 5–6 mm long, 1.3–2.3 mm wide; receptacle cylindrical to narrowly conic, 1–2 mm tall, 0.6–1 mm wide; paleas scarious, yellow-gold, lanceolate, the margins minutely lanciniate, strongly folded at the base and clasping the achenes, 4–6.5 mm long, 1–2 mm wide; florets 10–17 per head, the corollas yellow, hirtellous to glabrous, 3.5–5 mm long, 0.7–2 mm diam., the lobes 4–5, 1–1.6 mm long, the tube angular, flaring at the base, 1.1–2.2 mm long, the anthers exserted, lemon-yellow with ovate appendages, basally sagittate, the style branches revolute with obtuse tips. *Achenes* narrowly turbinate, angular, black, antrorsely hirsute, 1.5–2 mm long, 0.5–0.8 mm diam. with a wheel-shaped apical annulus; carpopodium present; pappus setose, of 15–25 stout bristles, 2.6–4.8 mm long.

Calea pittieri is a bushy to lianoid shrub of roadsides and savannas, flowering from October through February. *Calea pittieri* has often been confused with *Calea prunifolia* but the two may be distinguished most readily by differences in shape of the outer involucral bracts. The outer bracts of *C. pittieri* are oblong to narrowly ovate while those of *C. prunifolia* are ovate-oblong to rotund. The leaves of *C. pittieri* are smaller, more pubescent beneath, and the margins more divided than those of *C. prunifolia.* The peduncles, achenes, and pappus of *C. pittieri* are all shorter than those of *C. prunifolia.*

CANAL ZONE: Road to San Carlos, *Harvey 5151* (F). CHIRIQUÍ: Boquete, 4000 ft, *Davidson 840* (F, MO). Ca. 14 mi N of David, 1200 ft, *Lewis et al. 672* (GH, MO, UC, US). Alto Boquete, 1125 m, *Partch 69-39* (MO). N of Dolega, *Partch 69-141* (MO). Cerro Vaca, 900–1136 m, *Pittier 5299* (GH, US). Near Las Lagunas W of El Hato del Volcán, 1400 m, *Wilbur et al. 10995* (DUKE). COCLÉ: Vic. of El Valle, 600–1000 m, *Allen 1181* (F, GH, MO,

FIGURE 85. *Calea*.—A–B. *C. prunifolia* H.B.K.—A. Habit (× ½).—B. Head (× 2). [After *McDaniel 5175* (MO).]—C. *C. pittieri* B. L. Robinson & Greenman. Head (× 2). [After *Blum & Tyson 1875* (MO).]

US). Hills S of El Valle de Antón, 600–800 m, *Allen 2813* (GH, MO, US). Vic. of Río Teta and Interam. Hwy., *Blum et al. 1875* (FSU). Margarita, *Dwyer 8291* (MO). 2 mi E of Río Hondo, *Gentry 2909* (MO). Road to El Valle, *Harvey 5156* (F). Aguadulce, *McDaniel et al. 14761* (FSU); *Pittier 4901* (NY, US). 8.5 mi S of El Valle, 400 m, *McDaniel 8229* (DUKE, FSU). Between Aguadulce and Chico River, 20 m, *Pittier 5103* (US). W slope Cerro Campana, 2500 ft, *Tyson et al. 2368* (FSU, US). Vic. of La Mesa, *Tyson 6052* (FSU, MO). Río Hato Military Reservation along Interam. Hwy., *Tyson et al. 2554* (MO). Road to El Valle de Antón, *Wilbur et al. 15586* (DUKE). Slopes leading to El Valle de Antón, *Wilbur et al. 15594* (DUKE). COLÓN: Ca. 8 km NE of Santa Rita along ridge, 650 ft, *Wilbur et al. 10834* (DUKE, F, GH, MO, NY, US). HERRERA: Vic. of Chitré, ca. 20 m, *Allen 1109* (GH, MO, US). Vic. of Ocú, 100 m, *Allen 4054* (GH, MO). Road between Las Minas and Pesé, 900–1200 ft, *Burch et al. 1320* (F, GH, MO, NY, UC, US). Vic. of Ocú, 2 mi NW, *Stern et al. 33572* (MO, US). 10 mi S Ocú, *Tyson et al. 2859, 2860* (both MO). PANAMÁ: Vic. of Bejuco, *Allen 979* (MO). Nueva Gorgona, *Duke 4492* (GH, MO, US). Cerro Campana, *Lewis et al. 3031* (MO, UC). Cerro Campana, 500–600 m, *McDaniel 8093* (DUKE). VERAGUAS: 15.5 mi S of Santa Fe, *Gentry 2928* (MO). Ca. 5 mi NW of Santiago, *Wilbur & Teeri 13341* (F, GH, MO, NY). Ca. 17 mi NW of Santiago along Interam. Hwy., *Wilbur et al. 15469* (DUKE).

2. **Calea prunifolia** H.B.K., Nov. Gen. Sp. Pl. 4: 294. *tab. 406.* 1818. TYPE: Colombia, on the sides of the river Magdalena, near the town of Honda, 140 hex., June–Sept. 1801, *Humboldt & Bonpland s.n.* (P, holotype, not seen; B, isotype, not seen, photo US).—FIG. 85A–B.

A dense bushy to sprawling *shrub*, 1–5 m tall; stems terete to angular on younger branches, reddish brown, hirtellous to tomentose. *Leaves* opposite; blades elliptic to ovate, apically acute, basally short attenuate to rounded, often slightly oblique, the margins nearly entire to serrulate with the serrations callous tipped, 1.5–10.5 cm long, 1–6.8 cm wide, upper surface rugose, grey-green, shiny, hirsute to nearly glabrous, with 5 prominent veins, lower surface resin-dotted, pale green, hirsute; petioles tomentose, 0.5–1.7 cm long. *Inflorescences* of heads in terminal and axillary umbellate clusters; peduncles 0.5–4.0 cm long, grooved, hirsute to tomentose, resin-dotted. *Heads* discoid, campanulate, 3–10 mm wide, 6–13 mm tall; involucral bracts multiseriate, the outer bracts herbaceous, ovate-oblong to rotund, tomentose, resin-dotted, 0.6–3.6 mm long, 1–6 mm wide, the intermediate bracts ovate grading to oblong-ovate with rounded, squarrose, ciliate apices, scarious or herbaceous tipped, the inner bracts oblong, scarious, glabrous, or scattered hirtellous, 4.8–6.6 mm long, 1.4–2.3 mm wide; receptacle cylindro-conic, knobby, 1.2–2 mm tall, 0.7–1.2 mm wide; paleas scarious, golden yellow, lanceolate, with 2 small lobes, apically attenuate, the margins minutely laciniate and strongly conduplicate, clasping the achenes, 5.2–7 mm long, 0.7–1.6 mm wide; florets 10–20, the corollas yellow, glabrous, 4–6 mm long, 0.5–1.3 mm wide, the limb campanulate, the lobes 5, 0.8–1.8 mm long, the tube 1.2–2.4 mm long, flaring at the base, the anthers exserted, bright yellow, each with a narrowly ovate, acute appendage, the base sagittate, the style branches revolute, with weakly acute tips. *Achenes* narrowly turbinate, subterete to angular, black, antrorsely hirsute to nearly glabrous, 1.3–3 mm long, 0.3–0.8 mm wide, with a wheel-shaped annulus; carpopodium prominent; pappus of 20–25 stout attenuate bristles arising from a low crown, 3.7–6.3 mm long.

Calea prunifolia is a South American species ranging into Panama. It occurs as a dense bushy shrub or as a vine growing on trees at the forest edge. It is common in the sun in open thickets, on roadsides, and along the coastal bluffs. Flowering occurs from June through January.

BOCAS DEL TORO: Santa Catalina, *Blackwell et al. 2718* (MO). Almirante Chinguinola Canal, *Blum 1404* (MO, FSU). Laguna de Chiriquí, *Hart 174* (US). Isla Colón, 0–120 m, *von Wedel 510* (GH, MO). Vic. of Chiriquí Lagoon, *von Wedel 1181, 1414, 2477, 2731* (all GH, MO, US). CANAL ZONE: Fort Sherman, *Blum et al. 381* (FSU, MO). Ancón, road to Corozal, *Celestine 29* (US). Barro Colorado Island, *Croat 6729* (DUKE, MO, NY), *12278* (DUKE, F, MO, NY). Near Coco Solo weather station, *Duke 4289* (MO). Goofy Lake, 1–2 mi in direction of Cerro Jefe, 2000 ft, *Gentry et al. 3395* (MO). Manzanillo Island, *Hayes 689* (NY). Ancón Hill, 100–200 m, *Killip 12054* (GH, US), *39945* (US). Fort San Lorenzo, *McDaniel 5175* (FSU, MO). Ancón Hill, *Standley 25195* (GH, MO, US). Vic. of Fort Sherman, *Standley 31216* (US). Fort Sherman, *Tyson et al. 1208* (MO). Old Fort San Lorenzo, *Tyson 1576* (FSU, MO). COLÓN: Vic. Río Piedras along road to Portobelo, *Blum et al. 2539* (FSU); *Dwyer 2539* (MO). Portobelo, *Dwyer 4399* (GH, MO). Mouth of Río Piedras, *Lewis et al. 3178* (DUKE, MO, UC). DARIÉN: Chepigana, *Duke et al. 273* (MO, US). PANAMÁ: Vic. of Bejuco, *Allen 979* (F, GH). Cerro Campana, *Bartlett 16923* (DUKE, GH, MO). Ca. 7 mi N Cerro Azul on road to Cerro Jefe, ca. 2600 ft, *Blum et al. 1815* (FSU). Isla del Rey, *Correa 114* (DUKE). 3–4 mi N beyond Goofy Lake in Cerro Azul, *Correa et al. 440* (DUKE, FSU, MO). Beyond Goofy Lake along road to Cerro Jefe, *Correa et al. 578* (DUKE, MO, US). Between Panamá and Chepo, *Dodge et al. 16645* (MO). Panamá Viejo, *Duke 5726* (MO). Cerro Campana, 2400–2700 ft, *Duke 8682* (MO, US). Isla del Rey, *Duke 9530* (MO). San José Island, *Duke 12512* (MO). Isla de la Bayonetta, *Dwyer 1734* (MO). Cerro Azul, *Dwyer 1963* (FSU, NY). 8 mi S Goofy Lake toward Cerro Jefe, *Dwyer 7066* (GH, MO, UC, US). La Campana, Cerro Campana, *Ebinger 916* (MO). San José Island, *Erlanson 394* (GH, NY, US); *Harlow 19* (GH, US); *Johnston 29* (GH, MO, US), *1038* (GH). Cerro Campana, *Lewis et al. 3031* (DUKE). NE of Panama City, *Paul 198* (US). N of Panama City, *Paul 555* (MO, US). Sabana de Juan Corso, near Chepo, 60–80 m, *Pittier 4538, 4674* (both GH, US). Carretera de Nuevo Emperador, *Rodriguez 18* (DUKE, MO). Las Sabanas, *Standley 25921* (US). Corozal road near Panamá, *Standley 26807* (US). Vicinity of Juan Franco Race Track, near Panamá, *Standley 27744* (GH, US). Taboga Island, *Standley 27994* (US). Río Tapia, *Standley 28170* (US). Cerro Azul, 2000 ft, *Tyson 2071, 6327* (both FSU, MO). San José Island, *Tyson 5086* (DUKE, FSU, MO). SAN BLAS: Isla Soskatupo, *Duke 8514* (MO), *10193* (DUKE, MO). Ailigandí, *Dwyer 6806* (MO). Soskatupu, 0–150 ft, *Elias 1665* (GH, MO, US). Isla Pino, near Mulatupo, *Elias 1713* (GH, MO). VERAGUAS: Mouth of Río Concepción, *Lewis et al. 2842* (DUKE, MO, UC). PROVINCE UNKNOWN: *Hayes 21* (GH). Camino de Las Sabanas, *Heriberto 198* (GH, NY, US). *Seemann* (GH).

3. **Calea urticifolia** (Miller) DC., Prodr. 5: 674. 1836. TYPE: Mexico, Vera Cruz, *Houstoun* (not seen).

Solidago urticifolia Miller, Gard. Dict., ed. 8, no. 30. 1768.

Mocinna serrata Lag. Gen. Sp. Pl. Nov. 31. 1816. TYPE: Mexico, near Salmanticam, *Née* (not seen).

Caleacte urticifolia R. Brown, Trans. Linn. Soc. London 12: 109. 1817, nom. inval., not accepted by the author in the original publication.

Galinsogea serrata (Lag.) Spreng., Syst. Veg. 3: 579. 1826.

Calea cacosmioides Less., Linnaea 5: 157. 1830. TYPE: Mexico, *Schiede 351* (not seen, MO, photo).

C. axillaris DC., Prodr. 5: 673. 1836. TYPE: based on *Moccina serrata* Lag.

C. pellucidinerva Klatt, Bull. Soc. Roy. Bot. Belgique 31: pt. 1, 207. 1892. SYNTYPES: Costa Rica, *Pittier 3707* (not seen); *Pittier 3726* (US).

C. axillaris var. *urticaefolia* (DC.) B. L. Robinson & Greenman, Proc. Amer. Acad. Arts 32: 27. 1896.

C. urticifolia var. *axillaris* (DC.) Blake, Contr. Gray Herb. 3: 57. 1917.

Shrub 1.5–3.5 m tall; stems terete, striate, purplish, glabrous below to tomentose on younger branches. *Leaves* opposite; blades ovate to lance-ovate, acute to attenuate at the apex, rounded to somewhat cuneate at the base, the margins nearly entire on smaller leaves or dentate, crenate-serrate to sharply serrate with callous-tipped teeth, 3–13 cm long, 1.4–8 cm wide, the upper surface rugose, dark green, usually scabrous or glabrate, prominently 3-veined, the lower surface resin-dotted, pale green, scattered hirsute, denser on the veins; petioles 0.4–1.5 cm long, grooved, hirsute. *Inflorescences* of heads in terminal and axillary umbellate clusters on narrow branches; peduncles 0.2–2.5 cm long, tomentose. *Heads* radiate, campanulate, 6–13 mm wide (including rays), 8–10 mm tall; involucral bracts multiseriate, the bracts of the outer 2 or 3 series herbaceous or less often only herbaceous tipped, the outermost bracts lanceolate, 2.5–7.3 mm long, 1.1–3 mm wide, abaxially scabrous, adaxially resin-dotted, scattered hirsute, the intermediate bracts grading to broadly ovate, apically acute, the margins ciliate and often reddish-purple, scarious, the inner series narrower and longer, lance-ovate to oblong, the innermost bracts often bright yellow, 4.5–6.5 mm long, 1.7–2.2 mm wide; receptacle short conic, 1.2 mm tall, 1 mm wide, knobby; paleas scarious, lanceolate, with or without 2 short lateral lobes, folded and enclosing the disc achenes, 5–6.3 mm long, 1.5–2.5 mm wide; ray florets 4–7, pistillate, fertile, the ligules creamy-white to yellow, oblong, shallowly to deeply 2–3(–4)-lobed, gland dotted, 2.7–6 mm long, 1–3.2 mm wide, the tube 2–3 mm long, flared at the base, glabrous, the style branches bifid, revolute, acute; disc florets numerous, fertile, the corolla yellow, glabrous, the limb campanulate, the lobes 4–5, 1–1.6 mm long, the tube 1.7–2.5 mm long, flaring at the base, anthers exserted, yellow, the appendages narrowly ovate, sagittate at the base, the style branches recurved with obtuse tips. Ray *achenes* 1.2–2.3 mm long, 0.3–0.7 mm diam., narrowly turbinate, subterete to angular, black, sparsely antrorsely hirsute, with brownish hairs, carpopodium present, pappus setose, of 10–20 bristles 2.3–3.7 mm long; disc achenes like those of the ray florets but longer and more densely hirsute, 2–2.7 mm long, 0.5–0.8 mm diam., annulus 0.2–0.3 mm tall, pappus like that of the ray achene but longer, 2.5–4.3 mm long, occasionally purple at the base. Chromosome number $n = 19$, ca. 19 (Powell & Turner, 1963; Turner & Flyr, 1966).

Calea urticifolia ranges from Durango, Mexico through Central America to Panama. The species is weedy, occuring in dry savannas, thickets, forests, along roadsides, and in cultivated areas. Flowering occurs from November through June.

CANAL ZONE: Banks of Quebrada La Palma and cañon of Río Chagres, 70–80 m, *Dodge et al. 17335* (GH, MO, NY). Las Cruces Trail, 75 m, *Hunter et al. 708* (MO). Around El Paraíso, 30–100 m, *Pittier 2578* (F, GH, NY, US). Balboa, *Standley 29254, 29280* (both GH, US), *32144* (US). Río Chagres, between junction with Río Pequení and Río Indio, 66 m, *Steyermark et al. 16780* (MO). 10 mi S Ocú, *Tyson et al. 2807* (MO). CHIRIQUÍ: El Huacal, Boquete, *Atencio 21* (MO). From Boquete to 3 mi N, 3300–4200 ft, *Lewis et al. 573* (GH, UC, US). COCLÉ: Vic. of El Valle, 800–1000 m, *Allen 77* (GH, US). El Valle de Antón, 1000–2000 ft, *Lewis et al. 2600* (DUKE, UC). HERRERA: 4 mi S Los Pozos, *Tyson 2680* (FSU, MO). PANAMÁ: Augarubia, *Killip 3356* (US). Bella Vista, *Standley 25344* (US). Between Matías Hernández and Juan Díaz, *Standley 31967* (GH, US). PROVINCE UNKNOWN: *Haenke s.n.* (F). *Halsted s.n.* (NY).

85. GALINSOGA

Galinsoga Ruiz & Pavon, Fl. Peru Prodr. 110. *tab. 24.* 1794. LECTOTYPE: *G. parviflora* Cav.

Wiborgia Roth, Catal. Bot. 2: 112. 1800, nom. rejic. not *Viborgia* Moench 1794, nom. rejic., nor *Wiborgia* Thunberg 1800, (Leguminosae), nom. cons. TYPE: *W. acmella* Roth.
Galinsogea Attributed to Ruiz & Pavon in Willd., Sp. Pl. 3: 2228. 1803. Orthographic variant of *Galinsoga* Ruiz & Pavon.
Vigolina Poiret in Lam., Encycl. Meth. 8: 613. 1808. TYPE: *V. acmella* (Roth) Poir, substitute name for *Wiborgia* Roth, nom. rejic.
Galinsogaea Attributed to Ruiz and Pavon in Zucc., Flora 4: 612. 1821. Orthographic variant of *Galinsoga* Ruiz & Pavon.
Vargasia DC., Prodr. 5: 676. 1836, not Bertero ex Spreng. 1825. TYPE: *V. caracasana* DC.
Stemmatella Wedd. ex Benth. in Benth. & Hook., Gen. Pl. 2: 193. 359. 1873. TYPE: *S. congesta* Wedd. ex O. Hoffm.

Annual *herbs*, erect, decumbent or procumbent; stems 0.1–6 dm tall, often rooting at the lower nodes, branching, striate, green, reddish-green or red, sparsely to densely pubescent with multicellular trichomes. *Leaves* opposite, petiolate or sessile, entire to dentate-serrate, often ciliate, narrowly oblong to broadly ovate, glabrate to densely pubescent, with 3 principal veins, the bases connate around the stem. *Inflorescences* loose to congested cymose clusters of heads; peduncles slender, strigose and hispid-pilose, often with glandular capitate trichomes intermixed, axillary or terminal. *Heads* radiate or discoid, 3–8 mm tall, 3–20 mm wide, campanulate; involucral bracts biseriate, imbricate, 1–3 smaller, ovate outer bracts, deciduous or persistent, glabrous or sparsely pilose, the inner bracts more broadly ovate, each deciduous with 2–3 attached adjacent paleas enclosing a ray floret or not, 3–5-nerved, green or with light to dark red-purple tips, glabrous or pilose, slightly to strongly convex, the margins minutely laciniate, ciliate, or entire; receptacle convex to conical, 0.4–3.8 mm tall, 0.7–2.2 mm wide; paleas scarious, linear or narrowly to broadly lanceolate-oblanceolate, entire to deeply trifid, the margins minutely laciniate, sometimes purple-tipped, deciduous or the innermost paleas persistent; ray florets fertile, 3–5 or 8–10, the corolla white, pink, reddish-purple, the ligule wanting or quadrate to oblong, shallowly to deeply trifid, 0.5–7 mm long, 0.3–7 mm wide, the lobes subacute to obtuse, occasionally bilabiate, the tube pubescent, the style bifid with recurved branches, obtuse to acute; disc florets numerous, fertile, perfect or a single outer row of disc florets pistillate, the corolla tubular to campanulate, yellow, yellow-green or red-purple above with yellow below, 1.2–2 mm long, deciduous, lobes 5, acute, erect or reflexed, the limb hirtellous or glabrous, the tube short and pubescent, the anthers with ovate appendages, sagittate at the base, the style branches recurved, acute. Ray *achenes* turbinate, often compressed, glabrous to hispidulous, black, pappus coroniform or like that of the disc achene but usually shorter and present only on the side of the achene toward the interior of the head, sometimes wanting; disc achenes narrowly turbinate, subterete to somewhat angular, glabrous to hispidulous black, pappus of 10–20 linear-lanceolate, ovate to obovate, apically obtuse to acuminate or aristate scales with fimbriate, ciliate, or laciniate margins, or pappus coroniform or wanting. Chromosome number $x = 8$ (Turner & Flyr, 1966).

Galinsoga is a New World genus of about 16 species. *Galinsoga urticaefolia* (H.B.K.) Benth. and *G. parviflora* Cav. have become established as weeds in temperate areas world-wide. The remaining species are restricted in distribution to Mexico, Central America and South America. The species of *Galinsoga* are all very similar but may be distinguished by habit, leaf type, and features of the heads, such as ligule shape and size, type of pappus when present and shape of the paleas.

The genus *Galinsoga* may be distinguished from the other genera in the subtribe Galinsoginae by a combination of characters including, erect stems, generally small head size, white to purple ligules, the usual presence of 5 ray florets per head, and the usual enclosure of each ray floret in an ovate involucral bract and 2–3 adjacent scarious paleas. These structures: ray floret, involucral bract, and paleas, fall from the head as a single unit.

Literature:

St. John, H. & D. White. 1920. The genus *Galinsoga* in North America. Rhodora 22: 97–101.

Thellung, A. 1916. Über die in Mittleuropa vorkommenden *Galinsoga*-Formen. Allg. Bot. Zeitschr. Syst. 21: 1–16.

1. **Galinsoga urticaefolia** (H.B.K.) Benth. in Örsted, Vidensk. Meddel. Dansk Naturhist. Foren. Kjøbenhavn. 1852: 102. 1852.—Fig. 86.

Wiborgia urticaefolia H.B.K., Nov. Gen. Sp. Pl. 4. 257, *tab.* 389. 1818. TYPE: Ecuador, "Crescit juxta villam Marchionis de Miraflores, inter Mulalo et Pansache, 1700 hex., (Regno Quitensi.)," June, 1802, *Bonpland 3055* (P, holotype, US, photo).

Sabazia urticaefolia (H.B.K.) DC., Prodr. 5: 497. 1836.

Vargasia caracasana DC., Prodr. 5: 676. 1836. TYPE: Venezuela, Caracas, 1830, *Vargas 267* (G-DC, holotype, not seen, US, photo).

Galinsoga parviflora Cav. γ *hispida* DC., Prodr. 5: 677. 1836. SYNTYPES: "in Mexico circa urbem," *Berlandier 615* (P). "In Chilensibus montibus," *Haenke 1990* (PR, photo US).

Adventina ciliata Raf., New Fl. Bot. N. Amer. 1: 67. 1836. TYPE: not known.

Galinsoga hispida Benth., Bot. Voy. Sulph. 119. 1845. SYNTYPES: Colombia, Peyta (BM, not seen). Ecuador, Guayaquil, 1841, *Hinds s.n.* (K, US, photo). Peru, Lima, *Cuming 1028* (BM).

G. brachystephana Regel, Index Sem. Hort. Turic. 2. 1846. TYPE: not seen.

Wiborgia brachystephana (Regel) Heynh., Nom. Bot. Hort. 2: 707. 1846, pro syn.

Galinsoga hispida β *purpurascens* Fenzl, Del. Sem. Hort. Vindob. Advers. Bot. Strip. Sem. 4. 1851, pro syn.

G. parviflora var. *caracasana* (DC.) A. Gray, Smithsonian Contr. Knowl. 5: 98. 1853.

G. caracasana (DC.) Schultz-Bip., Linnaea 34: 529. 1866.

Stemmatella urticifolia (H.B.K.) O. Hoffm. ex Hieron., Bot. Jahrb. Syst. 28: 603. 1901.

Galinsoga humboldtii Hieron., Bot. Jahrb. Syst. 28: 618. 1901. TYPE: Locality not indicated, *Humboldt s.n.* (B, holotype, probably destroyed, US, photo; US, isotype fragment).

Stemmatella urticifolia var. *eglandulosa* Hieron., Bot. Jahrb. Syst. 36: 487. 1905. TYPE: Peru, near Cutervo, April 1879, *Jelski 609* (not seen).

Galinsoga quadriradiata Ruiz & Pavon var. *hispida* (DC.) Thell. Allg. Bot. Zeitschr. Syst. 21: 11. 1916.

G. quadriradiata var. *quadriradiata* f. *purpurascens* (Fenzl) Thell., Allg. Bot. Zeitschr. Syst. 21: 15. 1916.

G. quadriradiata var. *quadriradiata* f. *albiflora* Fenzl ex Thell., Allg. Bot. Zeitschr. Syst. 21: 15. 1916. SYNTYPES: Costa Rica, "prope San José ad fossam in campis sabanas dictis,"

5 June 1875, *Polakowsky 1* (not seen); "prope San José," July 1857, *Hoffmann 805* (not seen).

G. aristulata Bicknell, Bull. Torrey Bot. Club 43: 270. 1916, new name for *G. parviflora* var. *hispida*.

G. bicolorata St. John & White, Rhodora 22: 99. 1920. TYPE: Mexico, Chiapas, near Tumbala, 20 Oct. 1895, *Nelson 3356* (GH, holotype; US, isotype).

G. ciliata (Raf.) Blake, Rhodora 24: 34. 1922.

Sabazia urticaefolia var. *venezuelensis* Steyerm. Fieldiana, Bot. 28: 672. 1953. TYPE: Venezuela, Lara, slopes of mountain between Santo Domingo and Los Quebraditos, south of Las Sabanetas, above Humocaro Bajo, 8 Feb. 1944, *Steyermark 55379* (F, holotype, not seen; US, isotype).

Annual branching *herbs*, erect to spreading and rooting at the nodes, to 5.5 dm tall; stems green to reddish green, sparsely hirsute below to densely strigose and hispid-pilose above with multicellular trichomes, often with glandular capitate trichomes intermixed at the uppermost nodes. *Leaves* petiolate, ovate, ovate-lanceolate, 1.8–6 cm long, 0.5–4 cm wide, apically acute to obtuse, basally cuneate to somewhat rounded, the margins ciliate, serrulate to coarsely serrate, or crennate-serrate, sparsely to moderately hispid-pilose on both surfaces, prominently 3-veined. *Inflorescences* with peduncles 1–3.8 cm long, slender, green to reddish green, strigose and hispid-pilose often with multicellular glandular capitate trichomes, axillary or terminal, in cymose clusters. *Heads* radiate, campanulate, 2.9–7 mm wide; involucral bracts biseriate, imbricate, herbaceous, the margins minutely laciniate, the outermost bracts 1 or 2, narrowly to broadly ovate, 1–3.3 mm long, 0.9–1.5 mm wide, apically acute, glabrous or rarely sparsely hirsute, the inner involucral bracts 5, each subtending a ray flower and 2 attached outer paleas, broadly ovate, 2.5–3.5 mm long, 1.5–2.0 mm wide, convex, the margins minutely laciniate, acute, dark green or reddish purple, with dark veins, glabrous or sparsely glandular pilose; receptacle conic, 0.8–1.7 mm tall, 0.8–1.7 mm wide at the base; paleas scarious, the outermost narrowly ovate, the inner paleas lanceolate, entire to shallowly trifid, the margins minutely laciniate; ray florets 5, fertile, the corollas white, pink, or reddish purple, the ligule quadrate, 0.9–2.5 mm long, 1.1–2.5 mm wide, glabrous, with 3 obtuse lobes, occasionally bilabiate with 1 or 2 oblong inner lobelets to 1.2 mm long, the tube 0.5–1.1 mm long, pilose, the style branches recurved, apically acute; disc florets fertile, numerous, the corollas yellow, 5-lobed, acute, the limb tubular, hirtellous near the base to sparsely so on the lobes, 0.8–1.2 mm long, 0.4–0.7 mm wide, the tube hirtellous, 0.3–0.5 mm long, the style branches recurved, apically acute, the anthers yellow, 0.6 mm long, appendages ovate, basally sagittate. Ray *achenes* turbinate, compressed, black, 1.3–1.8 mm long, 0.6–0.8 mm wide, glabrous to strigose, the pappus coroniform, composed of 8–20 fimbriate, sometimes aristate scales, 0.2–1.1 mm long, or wanting; disc achenes turbinate, terete to subangular, black, 1.0–1.8 mm long, 0.4–0.7 mm wide, strigose, the pappus coroniform, of a few to 20 fimbriate, sometimes aristate, lanceolate scales, 0.2–1.2 mm long, or wanting. Chromosome number $n = 16$ (from Costa Rican material, Turner & King, 1964).

Galinsoga urticaefolia is a weedy species found commonly in disturbed habitats in the eastern United States, Mexico, Central America, South America, and Europe. The features of the achenes, pappus, and ray florets that historically have been used as characters to delimit species within the genus *Galinsoga* occur in a

FIGURE 86. *Galinsoga urticaefolia* (H.B.K.) Benth.—A. Habit (× ½).—B. Ray floret with involucral bract (× 6⁹⁄₁₀).—C. Disc floret (× 6⁹⁄₁₀). [After *Sawyer* 1 March 1967 (MO).]

greater variety of form in *G. urticaefolia* than anywhere else in the genus. Many new taxa have been described on the basis of characters which may be exhibited throughout their entire range of variability within a single population of *G. urticaefolia*. Except for ligule color, which is usually white in North America and often purple in South American plants, there is little geographical correlation with variability of morphological characters. For this reason no taxa below the specific rank are recognized.

I have not seen type material (MA) or photographs of *Galinsoga quadriradiata* and the possibility exists that this is the appropriate name for the Panamanian *Galinsoga*. The original description of *G. quadriradiata* is inadequate for purposes of identification.

Flowering occurs from December through August.

CHIRIQUÍ: Central valley of Río Chiriquí Viejo, 1800–2000 m, *Allen 1406* (GH, MO, NY, US). Cerro Punta, ca. 7000 ft, *Blum et al. 2432* (FSU, MO). Between Bambito and Cerro Punta, *Croat 10607* (MO). 2 mi N of El Hato del Volcán, *Croat 10640* (MO). Slopes of Las Cumbres near Cerro Punta, *Croat 13685* (MO). Between Boquete and Monte Rey, *Croat 15631* (MO). Vic. of Las Nubes, 2200 m, *Croat 22420* (MO). Along Río Chiriquí Viejo just above Guadeloupe, *Croat et al. 16050, 16051* (both MO). Ca. 2 mi below Boquete Lookout, *D'Arcy & D'Arcy 6310* (MO). Boquete Lookout, 4000 ft, *D'Arcy & D'Arcy 6322* (MO). Boquete, *D'Arcy & D'Arcy 6353A* (MO). La Popa above Boquete, 5200 ft, *D'Arcy & D'Arcy 6411* (MO). Bajo Chorro, 6000 ft, *Davidson 135* (F, GH, MO). Volcán de Chiriquí, 7000 ft, *Davidson 962* (MO). Río Chiriquí Viejo N of Volcán City, 5200–5600 ft, *Duke 9007* (MO). NW of Boquete, Cerro Horqueta, 5000–5800 ft, *Dwyer et al. 462* (MO). Boquete, *Dwyer et al. 7674* (MO); *Ebinger 648* (MO). Ca. 7 mi N of El Hato del Volcán, *King 5298* (US). Finca Collins, *Kirkbride 129* (MO, NY). From Boquete to 3 mi N, 3300–4200 ft, *Lewis et al. 387* (GH, MO, US). Alto Lino, 4200 ft, *Maurice 890* (US). Vic. Cerro Punta, 6800 ft, *Ridgway et al. 2389* (MO). Cerro Punta, *Sawyer s.n.* (WIS). Bambito, 5600 ft, *Tyson 5679* (FSU, MO). Above Bambito, ca. 6000 ft, *Tyson 5780* (FSU, MO). Vic. Boquete, 1700 m, *Wilbur et al. 11050* (DUKE). Between Cerro Punta and Las Nubes, *Wilbur & Teeri 13252* (DUKE). Along Río Caldera beyond Bajo Mono, *Wilbur et al. 13518* (DUKE). Volcán de Chiriquí, 1500–2000 m, *Woodson et al. 856* (GH, MO). Cerro Punta, ca. 2150 m, *Tyson 1023* (FSU). COCLÉ: Forest behind Club Campestre, 700 m, *Duke 13261(3)* (FSU, MO). DARIÉN: Cerro Pirre, 2500–4500 ft, *Duke et al. 13688* (MO).

86. JAEGERIA

Jaegeria H.B.K., Nov. Gen. Sp. Pl. 4: 278. 1820. TYPE: *J. mnioides* Kunth = *J. hirta* (Lag.) Less.

Aganippea Ses. & Moc. ex DC., Prodr. 6: 3. 1838. TYPE: *A. bellidiflora* Ses. & Moc. ex DC.
Heliogenes Benth., Pl. Hartw. 42: 1840. TYPE: *H. reglae* Benth.
Macella C. Koch, Ind. Sem. Hort. Berol. 1855. TYPE: *Acmella hirta* Lag.

Annual or perennial *herbs* of moist places, often rooting at the decumbent lower nodes; stems 0.5–10 dm tall, branching, striate, and glabrate to pubescent. *Leaves* opposite, petiolate or sessile, entire to dentate-serrate, linear to ovate, glabrous or pubescent, mostly with 3 principal veins, the bases connate around the stem. *Inflorescences* solitary heads or cymose clusters of a few to many heads; peduncles slender, glabrous to densely pubescent, axillary or terminal. *Heads* radiate, ca. 1 cm tall, 2.3 cm wide, campanulate; involucral bracts free, equal to subequal, 5–22, in 1–2 series, deciduous, linear to lanceolate, 0–4 nerved, glabrous to densely pubescent, flattened to convex, the margins expanded below into hyaline

often ciliate wings enclosing the ray achenes, the wings sometimes reduced or wanting; receptacle conical; paleas scarious (with corky thickenings in *J. sterilis*), the margins short to long ciliate, narrow to broadly lanceolate-oblanceolate, enclosing the achenes or sometimes narrowly linear and not enclosing the disc achenes, persistent or deciduous; ray florets fertile or sterile, equal in number to the involucral bracts, the corollas purplish, pink, yellow or white, the ligules narrowly oblong to spatulate, with or without a tube, apically entire to shallowly 3-lobed, the style branches recurved, obtuse to rounded; disc florets numerous, perfect, fertile, the corollas tubular, yellow or yellow-green, deciduous, (4)5-lobed, acute, the limb glabrous, the tube short, pubescent, with a thickened basal enlargement, the anther appendages acute, free-sagittate at the base, the style branches recurved or inwardly flattened, apically obtuse to rounded. Ray *achenes* turbinate to linear, mostly terete, glabrous and minutely striate, shiny black, with a shallow annulus at the apex, epappose; disc achenes resembling those of the ray florets, somewhat compressed or angular, epappose. Chromosome number $x = 9$ (Torres, 1968).

Jaegeria is New World genus of 9 species ranging from northern Mexico through Central America as far south as Uruguay. The one Panamanian species, *J. hirta*, is a highly variable weedy species occurring from northern Mexico to Uruguay. Of the other species, 5 are restricted to Mexico, 2 to the Galapagos Islands, and 1 to Colombia.

Literature:

Torres, A. M. 1968. Revision of *Jaegeria* (Compositae-Heliantheae). Brittonia 20: 52–73.

1. **Jaegeria hirta** (Lag.) Less., Syn. Gen. Comp. 223. 1832.—Fig. 87.

Acmella hirta Lag., Gen. Sp. Pl. Nov. 31: 1816. TYPE: Based on an unknown specimen originally at MA, but presumed lost.

Jaegeria mnioides H.B.K., Nov. Gen. Sp. Pl. 4: 278, *tab. 400*. 1820. TYPE: Mexico, near Aria, Michoacán, 1000 hex., *Bonpland* (not seen).

J. bellidioides Spreng., Syst. Veg. 3: 591. 1826. TYPE: Uruguay, Montevideo, *Sellow s.n.* (B, holotype, destroyed; P, lectotype, not seen).

J. parviflora DC., Prodr. 5: 544. 1836. TYPE: "Mus. Imp. Brasil" no. 433 (P, not seen).

J. repens DC., Prodr. 5: 544. 1836. TYPE: Brazil, near Serra dos Orgaos, Rio de Janeiro, *Vauthier* 323 (G-DC, not seen, photo KANU).

Spilanthes mariannae DC., Prodr. 5: 623. 1836. TYPE: Brazil, near Marianna, Minas Gerais, *Vauthier* 322 (G-DC, not seen).

S. karvinskiana DC., Prodr. 5: 623. 1836. TYPE: Mexico, *Karvinski s.n.* (G-DC, not seen).

S. ecliptoides Gardn., London Jour. Bot. 7: 407. 1848. TYPE: Brazil, Perma de Pao, Minas Gerais, *Gardner* Oct. 1840 (K; GH, drawing, not seen).

S. sessilifolia Hemsl., Biol. Centr. Amer., Bot. 2: 193. 1881. TYPE: Mexico, Orizaba, *Sallé 41* (K, not seen).

Jaegeria hirta var. *glabra* Baker, Fl. Bras. 6(3): 1967. 1884. TYPE: Brazil, *Mandon 80* (K, not seen).

J. discoidea Klatt., Jahrb. Hamb. Wiss. Anst. 102: 126. 1893. TYPE: Mexico, Sierra de las Cruces, 1 Oct 1892, *Pringle 4279* (MO, MSC, US, none seen).

Annual, little to profusely branching *herbs*, erect to spreading and rooting at the lower nodes, to 5.5 dm tall; stems greenish-red, sparsely to densely hirsute with

spreading trichomes of ca. 5 cells, 1–1.5 mm long, more densely pubescent at the nodes. *Leaves* sessile to subsessile, elliptic to lanceolate-ovate, 0.9–6.2 cm long, 0.3–2.5 cm wide, apically acute to acuminate, basally obtuse to rounded, ciliate, entire to denticulate, sparsely to densely hirsute on both surfaces, green, lighter beneath, prominently 3-veined, more pronounced beneath. *Inflorescences* with peduncles 0.5–6.5 cm long, slender, flaring at the apex, hirsute, green to reddish, solitary, terminal or axillary, or in cymose clusters. *Heads* radiate, campanulate, 3–10 mm wide, 3–6 mm tall; involucral bracts uniseriate, free, 5–12, linear-lanceolate, trinerved, 0.6–1.2 mm wide, 2–5.2 mm long, usually densely hispid on the basal half, the wings hyaline, 1.2–2.2 mm long, the margins short ciliate to erose; receptacle narrowly conic, 1–3.4 mm tall, 0.6–1.7 mm wide at the base; paleas linear to obovate, the inner ones narrower, hyaline, generally glabrous, the outermost rarely hirsute, the margins ciliate, convex, enclosing the disc achenes; ray florets fertile, the corollas white to yellow, the ligule oblong to obovate with 2 prominent veins and 2-lobed, or varying to 4–5-veined and 3-lobed, glabrous, 1.3–5 mm long, 0.5–1.8 mm wide, the tube 0.3–0.8 mm long, the style branches recurved, acute; disc florets 12–76, fertile, the corollas yellow, funnelform, the lobes (4)5, acute, often black-dotted, 1–1.7 mm long, 0.3–0.8 mm wide, the tube narrow, ca. 0.3 mm long with a pubescent basal enlargement. Ray *achenes* shiny black, narrowly obovate, somewhat flattened, 0.8–1.8 mm long, 0.3–0.6 mm wide, minutely striate, glabrous, carpopodium present, epappose but with an annulus 0.1–0.2 mm high; disc achenes 0.9–1.5 mm long, 0.3–0.5 mm wide, shiny black, glabrous, narrowly turbinate, terete to somewhat angular, carpopodium present. Chromosome number $n = 18$ (Torres, 1968).

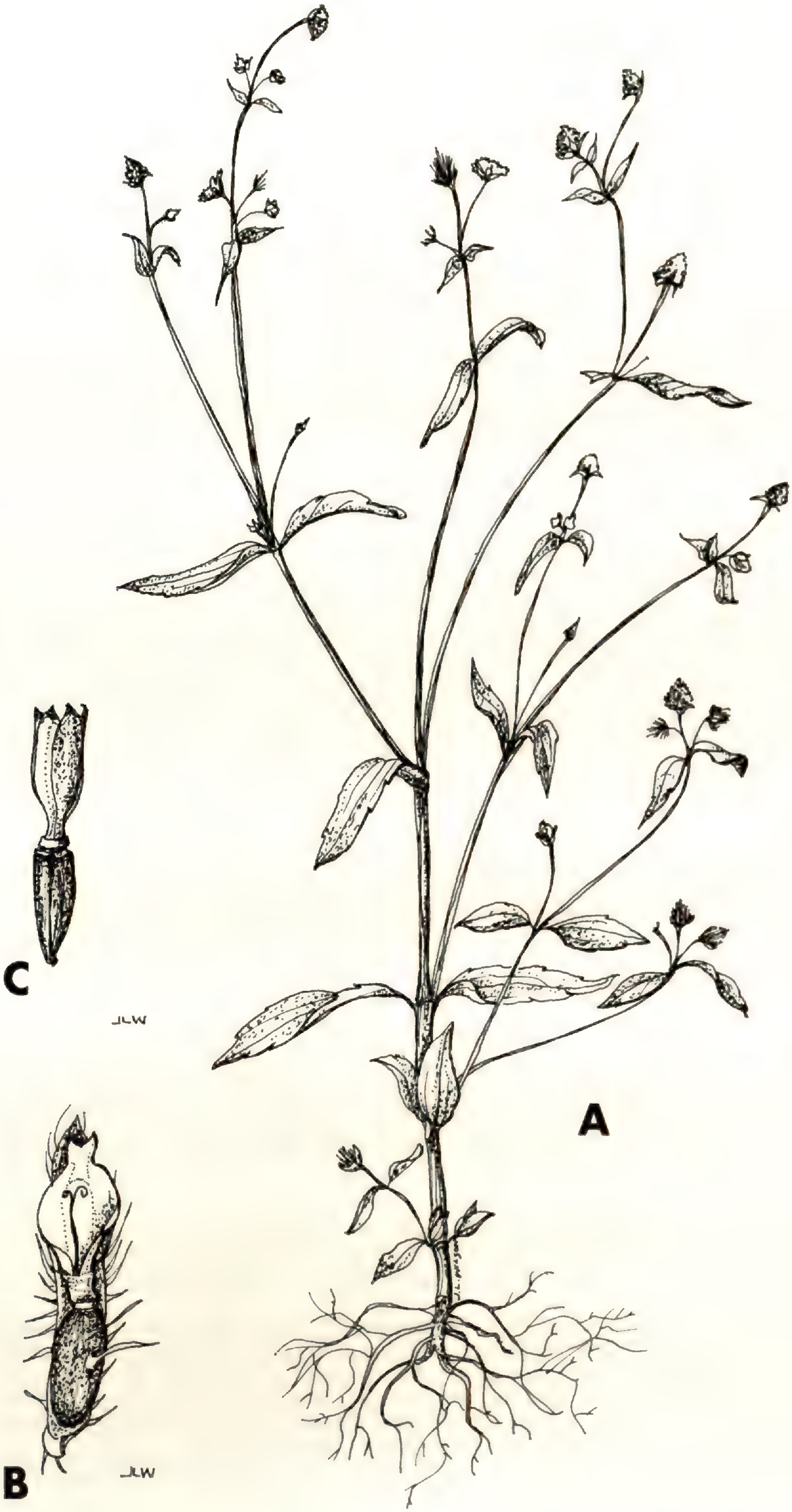
Jaegeria hirta is a common weedy species in Panama inhabiting moist disturbed areas. Although highly variable in respect to number and size of heads, involucral bracts (and ray florets) and number of disc florets, the variation is continuous, making varietal designations inappropriate. *Jaegeria hirta* is distinct in having rays to 5 mm long, densely hirsute involucral bracts which are longer than the paleas, and generally elliptic pubescent leaves.

Flowering occurs most commonly during the periods from December to March and June to August.

CHIRIQUÍ: Central valley of Río Chiriquí Viejo, 1800–2000 m, *Allen 1377* (F, GH, MO, NY, US). Vic. of Las Nubes, *Croat 22366* (MO). Along Río Chiriquí Viejo just above Guadelupe, *Croat et al. 16042* (MO). La Popa above Boquete, 5200 ft, *D'Arcy 6405* (MO). E side of Cerro Pando near Río Chiriquí Viejo, *D'Arcy 6640* (MO). Bajo Chorro, 6000 ft, *Davidson 136* (GH, MO). Lava fields near town of Volcán, *Duke 9171* (US). El Boquete, 1300 m, *Killip 3507* (US). From Boquete to 3 mi N, 3300–4200 ft, *Lewis et al. 323* (GH, MO). Vic. of El Boquete, 1000–1300 m, *Maxon 4998* (GH, US). Cerro Vaca, *Pittier 5314* (US). Cerro Punta, ca. 2150 m, *Tyson 1033* (FSU). W slopes of Volcán de Chiriquí, ca. 7500 ft, *Wilbur et al. 11021* (DUKE). Along Río Caldera beyond Bajo Mono, 1700 m, *Wilbur et al. 11048* (DUKE). Between Cerro Punta and Guadelupe, 1980 m, *Wilbur et al. 13050* (DUKE). Between Cerro Punta and Las Nubes, *Wilbur et al. 13264* (DUKE). 1 km N of Las Nubes, ca. 2000–2300 m, *Wilbur et al. 15191* (DUKE). Nueva Suiza, ca. 2.5 mi from Cerro Punta, *Wilbur et al. 15297* (DUKE). Río Caldera, ca. 2 mi up river from Boquete, *Wilbur et al.*

→

FIGURE 87. *Jaegeria hirta* (Lag.) Less.—A. Habit (× 9/10).—B. Ray floret (× 12⅗).—C. Disc floret (× 12⅗). [After *Lewis et al. 323* (MO).]


C
A
B

17264 (DUKE). Volcán de Chiriquí, ca. 1500–2000 m, *Woodson et al. 898* (GH, MO, NY, US). Vic. of Bajo Chorro, 1900 m, *Woodson & Schery 641* (MO). COCLÉ: Vic. of El Valle de Antón, *Croat 13291* (MO). W slopes of El Valle, *King* 5328 (UC, US). PANAMÁ: Cerro Azul, 2000 ft, *Tyson 2060* (MO).

87. SABAZIA

Sabazia Cass., Dict. Sci. Nat. 46: 480. 1827. TYPE: *S. humilis* (H.B.K.) Cass.

Eclipta sensu H.B.K., Nov., Gen. Sp. Pl. 4: 264. 1818. TYPE: *E. humilis* H.B.K.
Baziasa Steud., Nom. Bot., ed. 2. 1: 192. 1840. TYPE: *B. humilis* (H.B.K.) Steud.

Annual or perennial *herbs*; stems erect, decumbent or procumbent, arising from a caudex, occasionally rooting at the nodes, striate and grooved, glabrous to densely pilose, strigose or hirsute. *Leaves* opposite, petiolate or sessile; blades simple, ovate, obovate, elliptical, lanceolate or linear, the margins entire, serrate or denticulate. *Inflorescences* of solitary heads or of heads in few- to many-headed, loose to congested cymose clusters; peduncles terminal or axillary, to 20 cm long, slightly to densely pubescent, occasionally with glandular tipped trichomes. *Heads* radiate, campanulate or hemispherical; involucral bracts 1–4-seriate, imbricate, broadly ovate to linear-lanceolate, the outer series herbaceous, often purple at the apex, the inner series scarious; receptacle convex to conical; paleas scarious, lanceolate, entire to deeply trifid, acute to acuminate; ray florets fertile, 4–17, the ligules white above, often roseate below, oblong, obovate or quadrate, 3-lobed, the tube sparsely to densely pubescent; disc florets fertile, the corolla yellow, the limb cylindrical to campanulate, lobes 5, erect or reflexed, the tube sparsely pubescent, the anthers yellow or dark reddish brown, the appendages ovate, basally rounded or sagittate, the style branches terete or flattened on the inner surface, with acute or subulate tips. *Achenes* turbinate, obscurely ridged, glabrous or pubescent, black; carpopodium present; pappus of setose bristles, blunt broad scales, or absent. Chromosome number $x = 4$ (Longpre, 1970).

Sabazia is a genus of approximately 14 species. The genus is primarily Mexican in distribution with 3 species occurring in Central America and 2 species in Colombia.

Literature:

Fay, J. J. 1973. New species of Mexican Asteraceae. Brittonia 25: 192–199.
Longpre, E. K. 1970. The systematics of the genera *Sabazia, Selloa* and *Tricarpha* (Compositae). Publ. Mus. Michigan State Univ., Biol. Ser. 4: 283–384.

1. **Sabazia sarmentosa** Less., Linnaea 5: 148. 1830.

1a. **Sabazia sarmentosa** var. **papposa** (Blake) Canne, comb. nov.—FIG. 88.

Sabazia triangularis Blake, Proc. Amer. Acad. Arts 22: 615. 1924. TYPE: Panama, Chiriquí, around El Potrero Camp, Chiriquí Volcano, 2800–3000 m, 10–13 March 1911, *Pittier 3109* (US, holotype).
Sabazia triangularis var. *papposa* Blake, Ann. Missouri Bot. Gard. 26: 317. 1939. TYPE: Panama, Chiriquí, Loma Larga to summit, Volcán de Chiriquí, ca. 2500–3380 m, 4–6 July 1938, *Woodson et al. 1055* (US, holotype; MO, isotype).
Sabazia sarmentosa var. *triangularis* (Blake) Longpre, Publ. Mus. Michigan State Univ., Biol. Ser. 4: 356. 1970.

Perennial, procumbent or decumbent *herbs*, 20–90 cm tall; stems striate, greenish-red, glabrous below to strigose above, often rooting at the nodes. *Leaves* opposite; blades ovate to triangular-ovate, apically long acuminate, basally truncate to obtuse, 1.2–5 cm long, 0.5–2.6 cm wide, both surfaces appressed hirsute, the margins serrate. *Inflorescences* with heads terminal or axillary, solitary or in loose cymes; peduncles to 13 cm long, scattered hirsute below to densely hirsute near the heads, with interspersed glandular trichomes. *Heads* radiate, hemispherical to suboval, 1–2 cm wide, 0.5–1.1 cm tall; involucral bracts 2–3-seriate, herbaceous, the margins minutely laciniate, the outermost bracts ovate to lanceovate, 1.7–4.3 mm long, 1–2.2 mm wide, sparsely hirsute, the inner bracts elliptic-ovate to oblong-lanceolate, 3.5–7 mm long, 2–3.2 mm wide, slightly to moderately hirsute; receptacle convex to short conic; paleas scarious, 3.7–5.5 mm long, lanceolate, the inner paleas narrower, long attenuate, and with 1–2 small, acute or attenuate lateral lobes and minutely laciniate margins, the outermost paleas broader, obtuse to acute, attached in groups of 3 to the base of an inner involucral bract and enclosing a ray floret; ray florets 6–7, fertile, the ligules 3.6–7 mm long, 2.8–5.4 mm wide, white above, white to roseate below, obovate to subquadrate, trilobed, sparsely hirsute, denser along the base of veins, the tube 1.5–1.7 mm long, hirsute, the style branches oblique to recurved with obtuse tips; disc florets fertile, the corollas yellow, 2.5–3 mm long, the limb narrowly campanulate, hirtellous near the base to sparsely so above, the lobes 5, 0.5–1 mm long, the tube hirtellous, 0.7–1 mm long, the anthers exserted, the appendages ovate to elliptic-ovate, sagittate at the base, the style branches recurved with acute to subulate tips. Ray *achenes* obconical somewhat compressed, obscurely ridged, black, glabrous or strigose at the apex, ca. 2 mm long, 0.7–0.9 mm wide, pappus of a few bristles, short spatulate, fimbriate scales, or absent; disc achenes obconical, obscurely ridged, black, strigose on the margins or hispidulose over the entire surface, 2 mm long, 0.6–0.7 mm wide, carpopodium present, pappus of a few obovate to spatulate fimbriate scales, 0.5–1.2 mm long, or absent.

Sabazia sarmentosa var. *papposa* is endemic to the Volcán Chiriquí in Panama and the Cordillera de Talamanca in Costa Rica. It occurs along streams, in humid ravines, and in cloud forests from ca. 2500 to 3000 m. Flowering extends from January through July. *Sabazia sarmentosa* var. *papposa* is characterized by truncate leaf bases or a triangular ovate leaf shape, and achenes with trichomes distributed over the entire achenical surface.

CHIRIQUÍ: Las Cumbres, hogback ridge N of Quebrada, *Croat & Porter 16175* (MO). Bajo Chorro, 6000 ft, *Davidson 202* (MO, US). Volcán de Chiriquí, 10400 ft, *Davidson 1010* (MO, US). Around El Potrero Camp, Chiriquí Volcano, 2800–3000 m, *Pittier 3109* (US). Loma Larga to summit, Volcán de Chiriquí, *Woodson et al. 1055* (MO, US). Casita Alta to Cero Copete, 2300–3300 m, *Woodson & Schery 348* (MO).

88. TRIDAX

Tridax L., Sp. Pl. 2: 900. 1753; Gen. Pl. 382. 1754. TYPE: *T. procumbens* L.

Bartolina Adanson, Fam. 2: 124. 1763, nom. invalid.
Amellus Ortega ex Willd., Sp. Pl. 3: 2214. 1803, pro syn.
Balbisia Willd., Sp. Pl. 3: 2214. 1803, nom. rejic., *Balbisia* Cav. 1804, nom. cons. TYPE: *B. elongata* Willd.

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Sogalgina Cass., Bull. Soc. Philom. 31. 1818. TYPE: *Galinsoga trilobata* Cav.
Galinsogea H.B.K., Nov. Gen. Sp. Pl. 4: 252, *tab.* 386. 1818. TYPE: *G. trilobata* Cav.
Ptilostephium H.B.K., Nov. Gen. Sp. Pl. 4: 253, *tab.* 387–388. 1818. LECTOTYPE: *P. coronopifolium* H.B.K. (here chosen).
Carphostephium Cass., Dict. Sci. Nat. 44: 62. 1826. TYPE: *Ptilostephium trifidum* H.B.K.
Mandonia Wedd., Bull. Soc. Bot. France 11: 50, *pl. 1.* 1864. TYPE: *M. boliviensis* Wedd.

Annual or perennial *herbs* with slender taproots; stems procumbent, decumbent or erect, subscapose to leafy, sparsely to densely pubescent. *Leaves* opposite, or rarely alternate above, petiolate or sessile, simple, trilobed, pinnately lobed or divided, the margins entire, serrate, dentate to repand. *Inflorescences* with heads solitary or in few- to many-headed cymose panicles; peduncles slender to stout, elongate, pubescent, often with glandular-tipped trichomes. *Heads* discoid or radiate, campanulate (urceolate in *T. erecta*); involucral bracts 2–3-seriate and subequal in length to 4–5-seriate and obviously unequal in length, imbricate, greenish, often purplish at the apex, the inner bracts with scarious, purple margins; receptacle conical to convex or flattened; paleas scarious, persistent, rarely readily deciduous, partially enclosing the disc achenes, yellowish to yellow-green; ray florets fertile if present, the ligules white, yellow, roseate, or purple, obscurely to conspicuously bilabiate, the external lip with 2–4 shallow to deep lobes, the inner lobelets obvious to rudimentary, or wanting, the tube narrow, often pubescent; disc florets regular (except in *T. bilabiata* and occasionally in *T. coronopifolia* of Mexico), yellow, greenish-yellow, purplish, or whitish, the limb tubular or narrowly funnelform, glabrous or pubescent, the lobes 5, equal, sublanceolate, acute or obtuse, erect or reflexed, the anthers somewhat to nearly completely exserted, the appendages ovate, cordate, sagittate, or rhombic, the base sagittate, the style branches recurved to revolute, slender, subterete to flattened on the inner surfaces, with subulate tips. *Achenes* turbinate, narrowly obconic to subcylindric, terete to ridged, glabrous to densely pubescent with ascending hairs, pappus usually of ca. 20 plumose bristles or fimbriate, linear-lanceolate scales, rarely absent. Chromosome number $x = 9, 10$ (Powell, 1965).

Tridax is a genus of 27 species occurring in Mexico, Central America, and South America with the greatest number of species found in Mexico. It is distinguished from other members of the subtribe Galinsoginae by its generally bilabiate ray corollas (although this character also occurs occasionally in some *Galinsoga*), the long disc corollas, and chromosome numbers based on 9 and 10.

Literature:

Powell, A. M. 1965. Taxonomy of *Tridax* (Compositae). Brittonia 17: 47–96.

1. **Tridax procumbens** L., Sp. Pl. 900. 1753. TYPE: Mexico, Veracruz, *Houstoun* (BM, holotype, not seen).—FIG. 89.

Balbisia elongata Willd., Sp. Pl. 3: 2214. 1803. TYPE: "Herbarium Horti Botanici Matritensis, Plantae Novae Hispaniae," "*Amellus pedunculatus* N." (B, photograph of fragment, not seen).

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FIGURE 88. *Sabazia sarmentosa* var. *papposa* (Blake) Canne. Habit (× ½). [After *Davidson 1010* (MO).]

Amellus pedunculatus Ortega ex Willd., Sp. Pl. 3: 2214. 1803, pro syn.
Balbisia canescens Pers., Syn. Pl. 2: 407. 1807. TYPE: Colombia, Santa Marta, *Richard* (P, holotype, cf. Blake, 1930, not seen).
B. pedunculata Ortega ex Hoffmannsegg, Verz. Pfl. 228. 1824. TYPE: not seen.
B. divaricata Cass., Ann. Sci. Nat. 23: 90. 1831. TYPE: Grown from seed collected in "Maurice," probably introduced (not located).
Tridax procumbens var. *canescens* (Pers.) DC., Prodr. 5: 679. 1836.
T. procumbens var. *ovatifolia* B. L. Robinson & Greenman, Proc. Amer. Acad. Arts 32: 7. 1896. TYPE: Mexico, Oaxaca, vicinity of Yalalag, July 1894, *Nelson 948* (GH, holotype; US, isotype; neither seen).

Perennial, procumbent, trailing *herbs*, 14–40 cm tall; stems striate with woody bases, branching, often reddish, hirsute with multicellular trichomes, somewhat denser at the nodes. *Leaves* ovate to lanceolate, often lobed near the base, apically acute, cuneate to attenuate at the base, the margins nearly entire to serrate-dentate, undulate, 1–6 cm long, 0.5–4 cm wide, both surfaces hirsute, generally denser on the veins; petioles 0.2–2 cm long, the bases clasping the stem. *Inflorescences* solitary heads; peduncles 6–18.4 cm long, striate, hirsute with long spreading hairs, denser at the summit. *Heads* radiate, campanulate, 0.6–2.2 cm wide (including rays), 0.6–1.4 cm high; involucral bracts 2–3-seriate, the outer bracts ovate to oblong, 3.2–6.4 mm high, 1.5–3.6 mm wide, alternating bracts somewhat longer and wider, hirsute, acute to attenuate, the margins often purple, the inner bracts ovate to obovate, 4–8 mm long, 1.5–2.7 mm wide, hirsute, somewhat convex, the margins scarious and purple, cuspidate; receptacle short conical to nearly flat, 0.9–1.5 mm high, 3–4 mm wide; paleas persistent, scarious, lanceolate, with purple, minutely laciniate margins, cuspidate, 5–8 mm long, 0.8–1.7 mm wide, the inner paleas narrower; ray florets 3–6, fertile, the corollas pale yellow to white, the ligule oblong with 2 or 3 lobes, shallowly to deeply incised, hirsute on the 2 principal veins, 2–4 mm long, 1.2–4 mm wide, the tube 2–4 mm long, hirsute, the inner lobelets 1–2, lanceolate, 0.5–1.3 mm long, the style branches recurved; disc florets numerous, fertile, the corolla yellow and often purple tinged, 3.5–6.5 mm long, 0.6–1.4 mm wide, the limb narrow tubular, tapering to the tube, pilose at the base, with 5 lanceolate lobes, apically short hirsute, the tube 0.5–1.3 mm long with a ringlike thickening near the base, the style branches slender, flattened, revolute, with subulate tips. Ray *achenes* brown-black, narrowly obconical, obscurely angular, 1.5–2.5 mm long, 0.7–0.9 mm wide, densely ascending pilose, the carpopodium distinct, the pappus of plumose bristles, 0.7–2.5 mm long; disc achenes brownish-black, narrowly obconical, each with a narrow annulus at the apex, densely ascending pilose, the pappus of 18 to 20 plumose bristles, alternately longer and shorter, 3.5–6 mm long. Chromosome number $n = 18$ (Powell, 1965).

Tridax procumbens is a common weedy species in Panama and in tropical and subtropical areas of the world, although apparently native only to Mexico and Central America. Flowering occurs throughout the year.

BOCAS DEL TORO: Railroad track near station Milla 7.5, *Croat et al. 16437* (MO). Changuinola to 5 mi S at junction of Río Changuinola and Río Terebe, 1–200 ft, *Lewis et al.*

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FIGURE 89. *Tridax procumbens* L.—A. Habit (× ½).—B. Ray floret (× 5½).—C. Disc floret (× 5½). [After *Tyson 1398* (MO).]

A
B
C

925 (GH, UC, US). CANAL ZONE: Barro Colorado, *Bailey & Bailey 148* (GH). Farfan Beach, *Burch et al. 1408* (DUKE, F, GH, MO, UC, US). Alrededores de la represa de Miraflores, *Correa et al. 1180* (DUKE, FSU, GH, MO). Barro Colorado Island, *Croat 4169, 6025, 6799* (all MO). Behind Farfan Beach, *D'Arcy & D'Arcy 6071* (MO). Fort Kobbe, *Duke 3906* (GH, MO). Just E of Gatún locks, *Duke 4310* (MO). Navy Corrosion Lab., *Duke 4432* (MO). Culebra Island, *Duke 4628* (MO). Sosa Hill, *Duke 4664* (MO). Frijoles, *Ebinger 84* (MO, US). Barro Colorado Island, *Ebinger 136* (MO); *Foster 1375* (DUKE). Ancón, *Greenman & Greenman 5008* (GH, MO). Chagres River, ½ mi S of Gamboa, *Lazor 2258* (FSU). W side of Ferry Thatcher bridge, *Lazor 2888* (FSU, UC). 8 mi N of Gamboa, *Lazor 5273* (MO). ½ mi NW of Gamboa, ca. 70 m, *Liesner 1397* (MO). Barro Colorado Island, *Luteyn 788* (DUKE). Ancón, *Macbride et al. 13* (F, FSU, GH, US). Monte Lirio, *Maxon 6845* (GH, NY, US). Balboa, *Mell 7* (MO, NY). Ancón, *Piper 6005* (US). Between Corozal and Panamá, *Pittier 2172* (GH). Mamei Hill, 20–90 m, *Pittier 3797* (GH, US). Madden Dam area, *Porter et al. 4029* (MO). Balboa station, *Porterfield s.n.* (NY). Barro Colorado Island, *Shattuck 76* (GH, MO), 538 (MO). Sosa Hill, Balboa, *Standley 26418* (US). Hills N of Frijoles, *Standley 27634* (US). Barro Colorado Island, *Starry 117* (F, MO), *188* (MO). Miraflores Locks, *Stern et al. 66* (GH, MO, UC, US). Curundú, *Tyson 1088, 6244* (both FSU). Chiva Chiva Trail near Miraflores Lake, *Tyson 1398* (MO). Gatún railroad station, *Tyson 3520* (FSU, MO). Fort Amador causeway islands, *Tyson 5422* (FSU, MO). 1 mi SW of Cocoli, *Wilbur et al. 12937* (DUKE). CHIRIQUÍ: Burica Peninsula, Puerto Armuelles, *Busey 505* (MO). 1 mi W of airport at Puerto Armuelles, *Croat 21894* (MO). Río Majagua 3 mi above David, *D'Arcy & D'Arcy 6302* (MO). Boquete, *Davidson 692* (F, GH, MO, US). COCLÉ: Río Hato airstrip, *Burch et al. 1154* (GH, MO). Vic. of Olá, *Pittier 5041* (GH, US). 10 mi E Natá at Río Grande, *Tyson 5263* (DUKE, FSU), *5289* (FSU, MO). Between Las Margaritas and El Valle, *Woodson et al. 1719* (GH, MO). DARIÉN: Without definite locality, *Macbride 2678* (US). Peñas Bay near hotel, *Tyson 5542* (FSU, MO). LOS SANTOS: 3 mi S of La Palma, *Correa 77* (DUKE, MO). 2 mi S of Guarare, *Wilbur et al. 12176* (DUKE). PANAMÁ: Juan Díaz, *Castillo 20* (DUKE, GH, MO). Ca. 13 mi W of Chepo, *D'Arcy & D'Arcy 6034* (MO). Between Panamá and Chepo, *Dodge et al. 16696* (MO). San José Island, *Erlanson 133* (US), *552* (GH, US); *Harlow 25* (GH, US). Near Chepo, *Hunter et al. 53* (MO); *Pittier 4523* (US). Cerro Bandera, Las Cumbres, *Sandoval 60* (F). Taboga Island, *Standley 27094* (US); *Woodson et al. 1518* (GH, MO, NY, US). PROVINCE UNKNOWN: Vic. of Monkey Hill, *Cowell 25* (NY). Without definite locality, *Grisebach s.n.* (MO); *Hayes 690, 832* (both NY).

VI. TAGETEAE

DAVID J. KEIL[57]

Tageteae Cass., Jour. Phys. 88: 162. 1819. "Tagetineae." TYPE: *Tagetes* L.

Helenioideae subtribe Tagetineae (Less.) Benth. in Benth. & Hook. Gen. Pl. 2: 202. 1873. TYPE: *Tagetes* L.
Vernoniaceae subtribe Pectideae Less., Linnaea 5: 134. 1830. TYPE: *Pectis* L.
Senecionideae subtribe Tagetineae Less., Linnaea 6: 253. 1831. TYPE: *Tagetes* L.

Herbs or *shrubs*, usually strongly gland-dotted. *Leaves* mostly opposite, sometimes alternate, simple or compound. *Heads* radiate or discoid, few- to many-flowered; involucres of various shapes, the bracts in 1–3 series, distinct or fused; receptacle flat or convex, mostly naked, sometimes fimbrillate, never with chaff; florets white or yellow to purple, orange, red, or brown, the anthers basally cordate

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with elongate-deltoid or short-emarginate appendages, the style branches mostly elongate (in *Pectis* very short), smooth or papillate, appendaged or not. *Achenes* slender, cylindrical or clavate, terete or angled; carpopodium short to elongate; pappus of scales, awns, or bristles, or sometimes absent.

The Tageteae is a New World taxon of about 16 genera distributed in the warmer areas of both North and South America. All four of the largest genera of the tribe, *Dyssodia, Pectis, Porophyllum,* and *Tagetes,* occur in Panama. The most conspicuous feature of the various members of the Tageteae is the presence of pellucid oil glands on the foliage and usually on the involucral bracts as well. The oils of some of the taxa are strongly scented.

In the widely-followed systems of Bentham & Hooker (1873) and Hoffman (1894), the genera here included as the tribe Tageteae were placed in the catchall tribe Helenieae as subtribe Pectidinae (or Tagetinae). Cronquist (1955) argued that the sole unifying character of the Helenieae, the lack of receptacular chaff, is polyphyletic in origin, and consequently merged the Helenieae with the tribe, Heliantheae. For some genera traditionally placed in the Helenieae (e.g. *Gaillardia, Helenium*), such a transfer seems justified. For some other groups, particularly the well-defined Pectidinae, a placement in the Heliantheae is questionable. The Pectidinae have little in common with the remainder of the Helenieae (sensu lato). A better choice is to follow the lead of earlier workers (Cassini, 1826–1834; Rydberg, 1915) and the recent work of Strother (1969) and treat the Pectidinae as a tribe, the Tageteae. The differences separating the Tageteae from other tribes are at least as great as those separating the currently recognized tribes.

Literature:

Rydberg, P. A. 1915. (Carduales) Carduaceae: Helenieae, Tageteae. N. Amer. Flora 34: 81–180.

———. 1916. (Carduales) Carduaceae: Tageteae, Anthemideae. N. Amer. Flora 34: 181–288.

Strother, J. L. 1969. Systematics of *Dyssodia* Cavanilles (Compositae: Tageteae). Univ. Calif. Publ. Bot. 48: 1–88.

a. Involucre uniseriate.
  b. Involucral bracts united into a tube or cup ..... 92. *Tagetes*
  bb. Involucral bracts free or nearly so.
    c. Heads discoid; leaves petiolate, the blades broad ..... 91. *Porophyllum*
    cc. Heads radiate; leaves sessile, the blades linear or narrowly oblanceolate ..... 90. *Pectis*
aa. Involucre biseriate ..... 89. *Dyssodia*

89. DYSSODIA

Dyssodia Cav., Descr. Pl. Dem. 202. 1802. TYPE: *Tagetes papposa* Vent. = *Dyssodia papposa* (Vent.) Hitchc.

Willdenowa Cav., Icon. Descr. Pl. 1: 61, *tab.* 89. 1791, not *Willdenowa* Thunb. 1790. TYPE: *W. glandulosa* Cav.

Boebera Willd., Sp. Pl. 3: 2125. 1804. TYPE: *B. chrysanthemoides* Willd. nom. illeg.

Schlectendalia Willd., Sp. Pl. 3: 2125. 1804, nom rejic., *Schlectendalia* Less. 1830, (Compositae), nom. cons. TYPE: *Willdenowa glandulosa* Cav.

Adenophyllum Pers., Syn. Pl. 2: 458. 1807. TYPE: *Willdenowa glandulosa* Cav.
Thymophylla Lag., Gen. Sp. Pl. Nov. 25. 1816. TYPE: *T. setifolia* Lag.
Clomenocoma Cass., Dict. Sci. Nat. 9: 416. 1817. TYPE: *Aster aurantius* L.
Hymenatherum Cass., Bull. Soc. Philom. 1818: 183. 1818. TYPE: *H. tenuifolium* Cass.
Lebetina Cass., Dict. Sci. Nat. 25: 395. 1822. TYPE: *L. cancellata* Cass.
Rosilla Less., Syn. Gen. Comp. 245. 1832. TYPE: *R. lutea* Less.
Syncephalantha Bartl., Ind. Sem. Hort. Goett. 6. 1836. TYPE: *S. decipiens* Bartl.
Gnaphalopsis DC., Prodr. 7: 258. 1838. TYPE: *G. micropoides* DC.
Aciphyllaea (DC.) A. Gray, Mem. Amer. Acad. Arts, n.s. 4: 91. 1849. TYPE: *Dyssodia acerosa* DC.
Lowellia A. Gray, Mem. Amer. Acad. Arts, n.s. 4: 89. 1849. TYPE: *L. aurea* A. Gray.
Comaclinum Scheidw. & Planch. ex Planch., Fl. Serres 8: 19. 1852. TYPE: *C. aurantiacum* Scheidw. & Planch.
Boerbastrum (A. Gray) Rydb., N. Amer. Flora 34: 161. 1915. TYPE: *Dyssodia anthemidifolia* Benth.
Dysodiopsis (A. Gray) Rydb., N. Amer. Flora 34: 171. 1915. TYPE: *Dyssodia tagetoides* Torr. & A. Gray

Glabrous or pubescent annual or perennial *herbs* or *shrubs*, often strong-scented; stems few- to many-branched, depressed to erect. *Leaves* opposite or alternate, simple and entire to deeply pinnatisect or pinnately compound, variously punctate with oil glands. *Inflorescence* of few to many, solitary or cymosely clustered, sessile or peduncled heads, sometimes condensed into secondary heads; peduncles short to elongate, usually bracteolate. *Heads* radiate, or less commonly, discoid; involucres cylindric to campanulate, the bracts biseriate, distinct or variously fused, often subtended by an outer series of smaller bracts, variously punctate; receptacle flat to convex, fimbrillate; ray florets fertile, the corollas yellow, orange, red, or white, the ligules small to conspicuous; disc florets perfect and fertile, few to many, the corollas yellow to orange, regular or unequally lobed, the anthers subsagittate basally, the appendages deltoid-acute, the style branches elongate, variously appendaged. *Achenes* cylindric to obpyramidal, usually angled or ribbed, variously pubescent; carpopodium small, knoblike; pappus of awns, scales, coroniform, or absent. Chromosome base numbers $x = 7, 8, 13$ (Johnston & Turner, 1962; Strother, 1969).

Dyssodia is a mostly North American genus of about 33 species. Except for two taxa with amphitropical distributions, the genus does not reach South America. The primary center of diversity of the genus is Mexico. In Panama, the genus is represented by a single, somewhat anomalous species, *Dyssodia montana*. According to Strother (1969), *Dyssodia* is linked through *D. montana* to the small South American genus, *Schizotrichia* Benth. *Dyssodia montana* is also suspected of bridging the gap between *Dyssodia* and the Mexican genus, *Gymnolaena* Rydb. (Strother, 1967, 1969).

A recent revision by Strother (1969) has provided a much-needed updating of the nomenclature of *Dyssodia*. The only previous treatments of the genus of any comprehensive nature were those of Hoffman (1894) and Rydberg (1915), the latter complicated by a proliferation of ill-defined genera.

Literature:

Johnston, M. C. & B. L. Turner. 1962. Chromosome numbers of *Dyssodia* (Compositae-Tagetinae) and phyletic interpretations. Rhodora 64: 2–15.

Strother, J. L. 1967. Taxonomy of *Gymnolaena* (Compositae: Tageteae). Sida 3: 110–114.

1. **Dyssodia montana** (Benth.) A. Gray, Proc. Amer. Acad. Arts 19: 38. 1883. —FIG. 90.

Clomenocoma montana Benth., Pl. Hartw. 86. 1841. TYPE: Guatemala, in mountains of Aceytuno, near Guatemala, *Hartweg* 592 (K, holotype, not seen; LE, NY, P, isotypes, not seen).
Comaclinium aurantiacum Scheidw. & Planch., Fl. Serres 8: 19. 1852. TYPE: not seen.
Tithonia splendens Planch., Fl. Serres 8: 19. 1852, pro syn.
Dyssodia integrifolia A. Gray, Proc. Amer. Acad. Arts 19: 37. 1883. TYPE: Mexico, Chiapas, along streams in the mountains, 1864–1870, *Ghiesbrecht 784* (GH, holotype, not seen).
Gymnolaena integrifolia (A. Gray) Rydb., N. Amer. Flora 34: 161. 1915.

Perennial *herbs*, 0.3–2 m tall, arising from a woody caudex with thick fascicled roots; stems puberulent, at least above, stramineous to purplish, striate, sparingly branched. *Leaves* opposite, simple or rarely trifoliate, 2–10 cm long, sessile, or with winged petioles up to 1.5 cm long, narrowly to broadly lanceolate, elliptic, or ovate, apically acute to acuminate, basally rounded to cuneate, serrate, crenate or subentire, usually basally ciliate with 1–3 pairs of bristles or aristate lobes 2–8 mm long, pinnately veined, glabrous to densely puberulent on one or both surfaces, especially toward the base, conspicuously punctate on both surfaces with round, black oil glands. *Inflorescence* few-headed; peduncles terminal, 10–20 cm long, puberulent; bracteoles alternate, scattered, slender, 0.5–1 cm long, puberulent, usually punctate. *Heads* radiate; involucres hemispherical, 2–4 cm diam., the principal involucral bracts in 2 series, subequal, 1–1.4 cm long, distinct, oblong to obovate, broadly rounded and erose above, more-or-less indurate-keeled below, punctate with slender, elongate black oil glands, subtended by a graduated series of smaller, more slender bracts; receptacle rounded, fimbrillate with slender, aristate-tipped paleas 5–7 mm long; ray florets bright orange, conspicuous, the tubes slender, puberulent, 5–8 mm long, the limbs broadly ovate, 10–15 mm long, dark-purple veined; disc florets orange, 50–100, the corollas slender, 8–10 mm long, puberulent below, the limb glabrous, the lobes slender, ca. 3 mm long, the anthers ca. 3 mm long, the style branches ca. 2 mm long, slender, with short conic appendages. *Achenes* turbinate, 2–3 mm long, densely strigose; carpopodium conspicuous, knoblike; pappus of 30–40 scabrid bristles 3–7 mm long.

Dyssodia montana, with its large, orange heads and its simple, serrate leaves is distinctive. The leaf bases of this and a few related species bear elongate setiform lobes similar to those found in *Pectis* and in some species of *Tagetes*. This is another of the numerous characters which unite members of the tribe Tageteae.

The range of *D. montana* extends from southern Mexico south through Central America into Panama. In Panama, this species occurs in a broad range of altitudinal zones on the Pacific slope from Chiriquí to central Panamá. It flowers from November to February.

CANAL ZONE: El Valle, *Harvey 5162, 5178* (both F). CHIRIQUÍ: Cerro Vaca, 900–1136 m, *Pittier 5313* (US). Valley of upper Río Chiriquí Viejo, *White & White 101* (MO). COCLÉ: S of El Valle de Antón, 600–800 m, *Allen 2769* (GH, MO, US), *4209* (MO). El Valle de Antón, *Croat 13283* (MO); *Hunter & Allen 373* (MO). El Valle, *Lewis et al. 2586* (MO). Vic. of

FIGURE 90. *Dyssodia montana* (Benth.) A. Gray.—A. Habit (× ½).—B. Achene (× 4½).—C. Disc corolla (× 5). [After *Correa & Dressler 454* (MO).]

Olá, 100–350 m, *Pittier 5079* (GH, NY, US). Vic. of El Valle, *White & White 74* (MO). LOS SANTOS: 12 mi S of Macaracas, *Tyson & Blum 3065* (MO). PANAMÁ: Beyond Goofy Lake on road to Cerro Jefe, *Correa & Dressler 454* (MO). Between Cerro Jefe and Cerro Azul, *Croat 13063* (MO). Cerro Jefe, 3100 ft, *Dwyer & Gentry 9433* (NY). Without locality, *Hunter s.n.* (MO, UC). Road to Cerro Campana, 700 ft, *Tyson 6432* (MO, FSU). PROVINCE UNKNOWN: *Duke 6176* (MO).

90. PECTIS

Pectis L., Syst. Nat., ed. 10. 1221. 1759. TYPE: *P. ciliaris* L.

Seala Adanson, Fam. 2: 131. 1763. LECTOTYPE (here designated): *Pectis carthusianorum* Less.
Lorentea Lag., Gen. Sp. Pl. Nov. 28. 1816, not *Lorentea* Ortega, 1797. TYPE: *Pectis prostrata* Cav.
Cryptopetalon Cass., Bull. Soc. Philom. 1817: 12. 1817. TYPE: *C. ciliare* Cass.
Chthonia Cass., Dict. Sci. Nat. 9: 173. 1817. TYPE: *C. glaucescens* Cass.
Lorentea Less., Linnaea 5: 135. 1830, not *Lorentea* Ortega, 1797, nor Lag., 1816. TYPE: *Inula saturejaoides* Miller.
Pectidium Less., Linnaea 6: 706. 1831. TYPE: *Pectis punctata* Jacq.
Helioreos Raf., Atlantic Jour. 1: 145. 1832. TYPE: *Pectis angustifolia* Torr.
Pectidopsis DC., Prodr. 5: 98. 1836. TYPE: *Pectis angustifolia* Torr.
Tetracanthus A. Rich. in Sagra, Hist. Cuba 11: 60. 1850. TYPE: *T. linearifolius* A. Rich.
Cheilodiscus Triana, Ann. Sci. Nat. Bot., sér. 4, 9: 36. 1858. TYPE: *C. littoralis* Triana.

Glabrous or pubescent annual or perennial *herbs*, often strong-scented; stems slender, usually much branched. *Leaves* opposite, sessile, simple, narrow, usually entire, rarely toothed or lobed, 1-nerved, marginally ciliate with slender bristles, especially toward the base, variously punctate with oil glands. *Inflorescence* of open to condensed cymose clusters or solitary heads; peduncles short to elongate, with or without bracteoles. *Heads* small, radiate; involucres cylindric to campanulate, the bracts uniseriate, sometimes imbricate, distinct, thin-margined, indurate-keeled, apically ciliolate, variously punctate; receptacle convex, naked; ray florets fertile, equal in number to and individually subtended by the involucral bracts, the corollas yellow, ligulate; disc florets perfect and fertile, few to many, the corollas yellow, regular or weakly bilabiate, 4- or 5-lobed, the anthers weakly sagittate, the appendages short, truncate or emarginate, the style branches short, unappendaged, densely papillose. *Achenes* terete, weakly many-ribbed, glabrous or variously pubescent; carpopodium short, knoblike; pappus of scales, awns, bristles, coroniform, or absent. Chromosome base number $x = 12$ (Strother, 1969; Keil, in press).

Pectis is the largest genus in the Tageteae. The genus is well defined and has no close relatives among the other members of the tribe. *Pectis* may be distinguished from the other Panamanian members of the Tageteae by its slender, entire leaves and short style branches.

Pectis contains about 80 species distributed through much of the warmer portion of the New World. In Panama, *Pectis* is poorly represented with only 4 species. At least 2 species, *P. linifolia* and *P. uniaristata*, are distributed both to the north and to the south of Panama but have not been found in Panama.

Although *Pectis* has never been revised for the whole of its range, several useful partial revisions are available (Fernald, 1897; Urban, 1905; Rydberg, 1916; Keil, 1973).

Literature:

Fernald, M. L. 1897. A systematic study of the United States and Mexican species of *Pectis*. Proc. Amer. Acad. Arts 33: 57–86.

Keil, D. J. 1973. A re-evaluation of *Pectis* L. subgenus *Pectidopsis* (DC.) Fernald (Compositae: Pectidinae). Ph.D. dissertation, Ohio State University.

———. in press. Cytological investigations of North and Central American species of *Pectis* (Compositae: Tageteae). Rhodora.

Urban, I. 1905. Compositarum genera nonnulla. Symb. Antil. 5: 212–286.

a. Stems prostrate or decumbent.
   b. Heads subsessile; involucres falling entire; ray florets 5 ..... 3. *P. prostrata*
   bb. Heads conspicuously peduncled; involucral bracts falling separately; ray florets 5–8.
      c. Involucral bracts 3–4 mm long; diminutive annual of various habitats; stems not rooting at the nodes ..... 4. *P. swartziana*
      cc. Involucral bracts ca. 1 cm long; semisucculent, herbaceous perennial of seashores; stems elongate, creeping, rooting at the nodes ..... 2. *P. multiflosculosa*

aa. Stems erect.
   d. Peduncles mostly less than 10 mm long, ascending; inflorescences with heads tightly clustered ..... 1b. *P. elongata* var. *floribunda*
   dd. Peduncles more than 10 mm long, spreading; inflorescences more open ..... 1a. *P. elongata* var. *oerstediana*

1. **Pectis elongata** H.B.K., Nov. Gen. Sp. Pl. 1(4): 262. 1816. TYPE: Colombia, "Prope Popayan?," *Humboldt* or *Bonpland s.n.* (P, holotype, not seen, IDC Microfiche 6209. 111:II. 4; B, isotype, not seen, IDC Microfiche 1163:I. 6).

Erect annual or sometimes apparently perennial *herbs* 5–100 cm tall; stem terete or weakly angled, usually purplish, glabrous or minutely puberulent, usually much branched above. *Leaves* linear to narrowly oblanceolate, obtuse to acute, mucronate or aristate, basally ciliate with several pairs of bristles, glabrous to scaberulous on one or both surfaces, punctate on the undersurface with scattered small round oil glands. *Inflorescence* of few- to many-flowered cymose clusters or solitary heads; peduncles short to elongate, bracteolate. *Heads* small, radiate; involucres cylindric to narrowly campanulate, the bracts 5, little if at all imbricate, linear-oblanceolate, acute to acuminate, narrowly indurate-keeled, basally gibbous, glabrous, variously punctate; ray florets 5, the corollas 3–7 mm long, yellow or becoming reddish, glabrous, the tubes slender, the ligules usually involute; disc florets 5–9, the corollas 2–4 mm long, bilabiate. *Achenes* 2–3 mm long, black, short-strigillose; carpopodium short, knoblike; pappus of 2–20 scabrid bristles 2.5–4 mm long.

Pectis elongata is a widespread species in Latin America. There has been considerable confusion over the application of the name *P. elongata*, and several species have been described from various parts of the range of *P. elongata*. The recognition of some of these taxa is warranted on the basis of correlation between morphological variation and geographic distribution. These differences are insufficient to justify their distinction as separate species. Consequently, the combinations made below place these races at the varietal level under *Pectis elongata*.

Typical *P. elongata*, described originally from Colombia, does not occur in

Panama. This variety, distinguished primarily by its somewhat larger heads and 15–20 pappus bristles (fewer in the other varieties), apparently is restricted to northern South America. In Panama, the species is represented by two varieties, the Central American var. *oerstediana* and the primarily Caribbean var. *floribunda*. In some areas of Central America, these two varieties intergrade, but the Panamanian plants are usually easy to distinguish. Variety *oerstediana* is by far the more common in Panama.

1a. **Pectis elongata** var. **oerstediana** (Rydb.) Keil, comb. nov.—FIG. 91A–E.

P. oerstediana Rydb., N. Amer. Flora 34: 213. TYPE: Nicaragua, Chinadega, Realejo, 19 Jan. 1903, *Baker 2137* (US, holotype; GH, MICH, MO, MSC, ND-G, POM, UC, isotypes).

Mostly erect *herbs*, lemon-scented or with disagreeable odor; stems 10–100 cm long, usually purplish, often diffusely, much branched above. *Leaves* 1–4 cm long, 1–4 mm wide, with 2–11 pairs of bristles. *Inflorescence* cymosely, much branched; peduncles mostly 10–25 mm long. *Heads* radiate; involucres cylindric at anthesis but spreading in age, the bracts 4–5.5 mm long, with erect to spreading acuminate tips, smooth or minutely ciliolate, dotted with 3–6 pairs of narrow glands; ray corollas 3.5–5.5 mm long; disc corollas 2–3.5 mm long. *Achenes* 2–2.5 mm long; pappus mostly of 4–8 bristles 2–5 mm long. Chromosome number $n = 12$ (Keil, in press).

Pectis elongata var. *oerstediana* occurs only in Central America, extending from Guatemala to Panama. In some areas, a decoction of the plants is prepared as a medicinal beverage. The odor of some of the plants of this taxon has been likened by some collectors to that of stinkbugs (Pentatomidae) while other plants are lemon scented or combine both scents. In Panama, var. *oerstediana* is quite common on the Pacific slope from Chiriquí to central Panamá. It flowers primarily from October to January.

CANAL ZONE: Ancón Hill, *Paul 218* (US). Chiva-Chiva trail, Red Tank to Pueblo Nuevo, *Piper 5742* (GH, US). Sabana of Panamá, *Pittier 2543* (GH, NY, US). Balboa, *Standley 25297* (GH, US), *30902* (US). Corozal Road near Panamá, *Standley 26800* (US). Between Fort Clayton and Corozal, *Standley 29125* (US). CHIRIQUÍ: 14 mi N of David, *Lewis et al. 656* (GH, MO). COCLÉ: S of El Valle de Antón, *Allen 2809* (GH, MO, US). E of Río Teta and Interam. Hwy., *Blum & Tyson* (FSU, MO). Río Hato airstrip, *Burch et al. 1139* (DUKE, GH, MO, NY, UC, US). Aguadulce, *Pittier 4853* (US). Vic. of Olá, *Pittier 5084* (GH, NY, US). Penonomé and vic., *Williams 170* (NY, US). HERRERA: Vic. of Ocú, *Allen 4040* (MO). 4 mi S of Los Pozos, *Dwyer 2649* (MO). Ocú, *Ebinger 1088* (GH, MO). Vic. of Ocú, *Stern et al. 1695* (MO, US). Vic. of Las Minas, *Stern et al. 1810* (MICH, MO, US). 4 mi S of Los Pozos, *Tyson 2649* (FSU). 10 mi S of Ocú, *Tyson et al. 2879* (MO). PANAMÁ: Vic. of Pacora, *Allen 999* (MO). Between Capira and Potrero, *Dodge & Hunter 8619* (MO). Between Panamá and Chepo, *Dodge et al. 16650* (GH, MO, NY). Nueva Gorgona, *Duke 4541* (MO). Near Playa Río Mar, *Duke 11770* (DUKE, MO). Tocumen airport, *Dwyer 4005* (MO). Santa Clara, *Dwyer & Duke 8290, 8291* (both MO). San José Island, *Erlanson 571, 580* (both US). Llanos de Panamá Viejo, *Heriberto 287* (US). Near Chepo, *Hunter & Allen 16* (MO). San José Island, *Johnston 172* (GH, US). Near Alajuela, *Killip 3224* (GH, NY, US). Between Las Sabanas and Río Yguana, *Macbride 2660* (F, US). 7 mi S of Campana, *McDaniel 8315* (DUKE, FSU). Bayano River, *Mell s.n.* (NY, US). Sabana de Dormisolo near Chepo, *Pittier 4658* (NY, US). Matías Hernández, *Pittier 6886* (US). Bella Vista, *Standley 25364* (US). Las Sabanas, *Standley 25889* (GH, US), *25930* (US). Near Punta Paitilla, *Standley 26290* (MO, US). E of Río Tocumen, *Standley 26580* (US). Near Panamá, *Standley 27722* (GH, US). Río Tapia, *Standley 28187* (GH, US). Río Tocumen, *Standley 29476* (US). Tumba Muerto Road, near Panamá, *Standley 29766* (US). Nuevo San Francisco, *Standley*

A
D.K.
B
D.K.
C
D.K.
D
D.K.
E
D.K.
G
D.K.
H
D.K.
F
D.K.

30711, *30784* (both US), *30755* (US, in part). Between Las Sabanas and Matías Hernández, *Standley 31853* (US). Between Matías Hernández and Juan Díaz, *Standley 32089* (US). VERAGUAS: Vic. of Santiago, *Allen 1018* (F, GH, MO, US). PROVINCE UNKNOWN: *Seemann s.n.* (GH, K).

1b. **Pectis elongata** var. **floribunda** (A. Rich.) Keil, comb. nov.

P. floribunda A. Rich. in Sagra, Hist. Cuba 12: 36. 1850. TYPE: Cuba, *Sagra 19* (P, holotype).
P. plumieri Griseb., Fl. Brit. W. Ind. 378. 1864. TYPE: Jamaica, *McNab* TYPE: not seen, probably at GOET or K.

Tall, mostly erect, lemon-scented *herbs*; stems 10–50 cm tall, straw-colored or purplish, much branched, the branches ascending. *Leaves* 1–4 cm long, 1–3 mm wide, with 2–5 pairs of marginal bristles toward the base. *Inflorescence* cymosely much branched, the heads clustered at the stem tips; peduncles less than 10 mm long. *Heads* radiate; involucres cylindric, tardily spreading in age, the bracts 4–4.5 mm long, linear-oblanceolate, acuminate, glabrous, dotted with 3–5 pairs of narrow glands; ray corollas 3.5–4 mm long; disc corollas 2–2.5 mm long. *Achenes* 2–2.5 mm long; pappus of 4–8 bristles 3.5–4 mm long.

Pectis elongata var. *floribunda* is widespread in the Caribbean region and reaches the mainland in scattered localities from eastern Mexico to northern South America. In Panama, this variety is allopatric with var. *oerstediana*, occurring only in northern Bocas del Toro and eastern Darién Provinces. In other areas of Central America, these taxa sometimes intergrade. It flowers through much of the year.

BOCAS DEL TORO: Bocas, *Lazor et al. 2420* (FSU). Bocas del Toro Island Airport, *Lewis et al. 997* (GH, MO, NY, UC, US). Without definite locality, *von Wedel 335* (MO). Isla Colón, vic. of Chiriquí Lagoon, *von Wedel 2824* (GH, MO, US). DARIÉN: El Real, *Burch et al. 1072* (GH, MO, UC, US). Río Balsas between Manené and Guayabo, *Duke & Nickerson 14939* (MO).

2. **Pectis multifloculosa** (DC.) Schultz-Bip. in Seem., Bot. Voy. Herald 309. 1856.—FIG. 91F–H.

Lorentea multifloculosa DC., Prodr. 5: 102. 1836. TYPE: Peru, "in montibus Guanaccentibus," *Haenke s.n.* (G-DC, lectotype, here chosen IDC Microfiche 800. 788: II. 3; M, isolectotype, MO, photo).
Pectis arenaria Benth., Bot. Voy. Sulphur 110. 1845. SYNTYPES: Ecuador, Puna, near Guayaquil. Mexico, Guerrero, sands of the sea coast, Acapulco. Honduras, Conchagua (not seen).
Cheilodiscus littoralis Triana, Ann. Sci. Nat. Bot., sér. 4, 9: 36. 1858. TYPE: Colombia, Prov. Buenaventura, Amarales, *Triana*, May 1853 (P, holotype, not seen, F, photo).
Pectis bibracteata Klatt, Leopoldina 20: 92. 1884. TYPE: Mexico, St. Augustin, Oct. 1842, *Liebmann 465* (C, not seen).
P. maritima Ses. & Moc., Naturaleza (Madrid), ser. 2, 1: app. 143. 1890. TYPE: Mexico, "in arenosis Oceani Australis littoribus," Dec. (type not located, possibly at MA).
P. grandiflora Klatt, Bot. Beibl. Leopoldina 6. 1895. TYPE: Costa Rica, Hato Viejo, Jan. 1893, *Pittier 7342* (GH, holotype).

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FIGURE 91. *Pectis*.—A–E. *P. elongata* H.B.K. var. *oerstediana* (Rydb.) Keil.—A. Habit (× ½).—B. Involucral bract (× 5).—C. Achene (× 5).—D. Disc corolla (× 10).—E. Ray corolla (× 10). [After *Keil 9413* (OS).]—F–H. *P. multifloculosa* (DC.) Schultz-Bip.—F. Habit (× ½).—G. Achene (× 5).—H. Disc corolla (× 5). [After *Dwyer 2520* (MO).]

P. lehmannii Hieron., Bot. Jahrb. Syst. 28: 620. 1901. SYNTYPES: Ecuador, Bahia de Caraquer, Jan.–Feb., *Lehmann 7954* (B, probably now destroyed, F, photo). Colombia, *Triana 1401* (not seen).
P. falcata Cufod., Arch. Bot. Sist. 9: 202. 1933. TYPE: Costa Rica, "Peninsula Osa ad Golfo Dulce, prope Puerto Jimenez," 2 Apr. 1930, *Cufodontis 177* (GE, holotype, not seen, OS, photo; W, isotype).

Stout, prostrate, semisucculent, perennial, seashore *herb*; stems terete or weakly angled, usually purplish, creeping, rooting at the nodes, giving rise to short, densely leafy, floriferous lateral branches, glabrous or puberulent in lines. *Leaves* linear to oblanceolate, 2–3 cm long, 1–5 mm wide, obtuse to acute, mucronate, ciliate below with 4–7 pairs of long bristles, marginally puberulent to scaberulous, otherwise glabrous, punctate on the undersurface with submarginal rows of circular oil glands and sometimes with additional scattered glands. *Inflorescence* of solitary terminal heads; peduncles 1–3 cm long, leafy-bracted. *Heads* radiate; involucre campanulate, 10–12 mm high, 7–10 mm broad, the bracts 5–8, oblong to obovate, acute, strongly imbricate, indurate and gibbous at the base, longitudinally striate, marginally ciliolate, otherwise glabrous, inconspicuously punctate with scattered slender oil glands; ray florets 5–8, the corollas yellow, 10–12 mm long, glabrous, the tube ca. 3 mm long, the ligule elliptic, strongly nerved; disc florets 20–40, the corollas yellow, 7–8 mm long, bilabiate, sparsely glandular-puberulent below, the anthers 2.5 mm long, the appendage short, emarginate. *Achenes* narrowly clavate, dark brown to black, 8 mm long, glabrous; carpopodium short and blunt; pappus a crown of low scales, or some of the scales prolonged into slender scabrid bristles 3–7 mm long. Chromosome number $n = 36$ (Keil, in press).

Pectis multifloscula occurs on Pacific Ocean beaches from Peru to central Mexico. The width of the leaves, size of the heads, and structure of the pappus are all rather variable in this species, and this variation is reflected in the proliferation of names.

The horizontal stems of *P. multifloscula* sometimes extend for several meters just under the surface of the sand. This growth form is unique in the genus, indeed in the entire tribe. This species is one of the two known hexaploids in *Pectis* (Keil, in press) and the ancestry, if through allopolyploidy, is difficult to surmise.

At present, *P. multifloscula* is known from Panama only from two collections that flowered in August and September.

CHIRIQUÍ: Vic. of San Félix, *Pittier 5746* (GH). LOS SANTOS: Pocrí, *Dwyer 2520* (MO).

3. **Pectis prostrata** Cav., Icon. Descr. Pl. 4: 12. 1797. TYPE: Grown from seed at Royal Botanical Garden of Madrid, 1795 (holotype not located at MA; F probable isotype, cultivated at Madrid from seed collected by Née in Queretaro).

P. costata Ser. & Merc. ex DC., Prodr. 5: 100. 1836. TYPE: Cuba, *Sagra s.n.* (not seen).
P. prostrata var. *urceolata* Fern., Proc. Amer. Acad. Arts 33: 68. 1897. TYPE: Mexico, Chihuahua, Hacienda San José, 1885, *Palmer 53* (GH, holotype).
P. urceolata (Fern.) Rydb., N. Amer. Flora 34: 197. 1916.
P. multisetosa Rydb., N. Amer. Flora 34: 198. 1916. TYPE: Guatemala, Santa Rosa, Chupadero, 1892, *Heyde & Lux 4232* (NY, holotype).

Prostrate to ascending, much branched, often mat-forming, fibrous-rooted, annual *herbs*; stems several to many from the base, leafy, terete or round-angled, often purplish, diffusely much branched, pubescent in lines. *Leaves* linear to narrowly oblanceolate, 1–3 cm long, 1.5–5 mm wide, obtuse, mucronate, marginally ciliate sometimes to above the middle with 4–12 pairs of bristles, scaberulous on the margins, villous-ciliolate toward the base, otherwise glabrous, densely punctate on the pale undersurface with scattered, tiny round glands. *Inflorescence* of congested cymose clusters; peduncles 1–2 mm long, or heads sessile. *Heads* radiate; involucres cylindrical, ellipsoid or campanulate, 6–7 mm long, 3 mm wide, the bracts 5, oblong to obovate, obtuse to emarginate with spreading tips, imbricate, indurate-keeled to the tip, bowed out toward the middle, gibbous basally, glabrous, punctate in submarginal rows and sometimes also along the midrib with tiny elliptical glands; ray florets 5, the corollas bright yellow, 3.5–4 mm long, scarcely exceeding the involucres, spreading, but in dried specimens apparently ascending, glabrous, the slender tube ca. 1 mm long, the ligule narrowly ovate but often inrolled and appearing narrower; disc florets 6–15, the corollas yellow, 2.5 mm long, biliabiate, glabrous, the tube narrow, 0.7–1 mm long, the anthers 0.8 mm long with short, truncate appendages, the style branches scarcely exceeding the corolla lobes. *Fruit* consisting of involucre and enclosed achenes which fall together at maturity; achenes black, narrowly clavate, obscurely many-ribbed, 3–3.7 mm long, strigose to villous in lines; carpopodium small; pappus of 3–5 thin, whitish, lacerate-margined, long-acuminate scales 2–2.5 mm long. Chromosome number $n = 12$ (Keil, in press).

Pectis prostrata is apparently a recent introduction into Panama. Although the species occurs naturally from the southern United States to northern South America, it was not collected in Panama until 1969. It is known in Panama only from disturbed sites in the Canal Zone. *Pectis prostrata* is a common roadside weed through most of its range, and can be expected to spread along roads and other disturbed sites in Panama. Fortunately it does not become a nuisance in cultivated areas.

Pectis multisetosa, described by Rydberg from Guatemalan material, is a name that has been applied to a large-headed form of *P. prostrata* common in Central America. Other than in number of flowers, these plants do not differ significantly from typical *P. prostrata*. Because of intergradation in other areas of Central America, recognition of *P. multisetosa* as a species distinct from *P. prostrata* is not warranted. Further study may necessitate the recognition of these plants at the varietal level. Both the large-headed and the smaller-headed forms of *P. prostrata* have been collected in Panama.

CANAL ZONE: Curundú, *D'Arcy 6102* (MO); *Tyson & Lazor 5432* (FSU, MO). Albrook, *Tyson & Lazor 6015* (FSU).

4. **Pectis swartziana** Less., Linnaea 6: 711. 1831. TYPE: "ex India Occidentalis et Jamaica," *Swartz* Herb. Thunberg (UPS, holotype, not seen, IDC Microfiche 1036, 844:III:3).

P. pratensis C. Wright in Sauvalle, Anales Acad. Ci. Méd. Habana 6: 210. 1870. TYPE: Cuba, "en sabanas cerca de la hacienda de Puercos Gordos, jurisdiccion de San Cristobal," *Wright 3612* (F, isotype fragment).

P. panamensis Brandegee, Univ. Calif. Publ. Bot. 4: 192. 1911. TYPE: Panama, 50 mi S of the Canal Zone, *Bolivar Jurado s.n.* (UC, holotype).

Diminutive spicy-scented, prostrate, fibrous-rooted, annual *herb*; stems 5–25 cm long, leafy, much branched in age, glabrous or minutely puberulent in lines. *Leaves* linear to narrowly oblanceolate or elliptical, 6–23 mm long, 1.5–6 mm wide, obtuse to acute, mucronate, entire, with 1–3 pairs of bristles toward the base, glabrous or minutely scaberulous on the margins, punctate on the undersurface with numerous round oil glands. *Inflorescence* of loosely clustered heads; peduncles slender, 8–20 mm long, 3–5 bracteolate, glabrous. *Heads* small, radiate; involucres cylindric or narrowly campanulate, the bracts 5–8, linear, rounded, erose-ciliolate above, thin-margined, indurate-keeled, bowed out toward the middle, gibbous basally, glabrous, punctate with 2–3 pairs of slender submarginal glands and 1 or 2 rounded subterminal glands; ray florets 5–8, the corollas yellow or becoming purplish, 2.5–3.5 mm long, glabrous, the ligule ovate but usually inrolled and appearing narrower, about equalling the slender tube; disc florets 5–8, the corollas yellow or becoming purplish, 1.5–2 mm long, bilabiate, the anthers 0.7 mm long with a short emarginate appendage. *Achenes* cylindrical, weakly ribbed, black, 2.5–2.7 mm long, sparsely to densely strigillose; carpopodium short; pappus a short crown of fimbriate scales 0.5–0.7 mm long, rarely with one or more of the scales prolonged into bristles to 2.5 mm long. Chromosome number $n = 24$ (Keil, in press).

Pectis swartziana often grows as a roadside weed and with the foliage often concealed by that of associated plants is easily overlooked. It is probably more common than is indicated by the collections now available. This species occurs from southern Mexico to Panama and also is found on some of the Caribbean islands. It flowers from June to December.

CANAL ZONE: Fort Kobbe, *Duke 3913* (MO). CHIRIQUÍ: 2 mi S of Boquete Lookout, 3000 ft, *D'Arcy 6320* (MO). David airport, 25 ft, *Lewis et al. 734* (GH, MO, NY, UC). COCLÉ: Vic. of Natá, *Allen 833* (GH, NY). Penonomé, *Ebinger 1005* (F). Aguadulce, *Pittier 4937* (GH). PANAMÁ: Near Chepo, *Duke 6037* (MO). Sabana de San Juan Corso, *Pittier 4502* (GH, NY). Laguna de Portala, *Pittier 4623* (GH). Nueva San Francisco, *Standley 30755* (US, in part). Between Pacora and Chepo, *Woodson et al. 1658* (GH). VERAGUAS: 14 mi W of Santiago, *King 5275* (UC). 5 mi SE of Calobre, *Wilbur et al. 12127* (DUKE).

91. POROPHYLLUM

Porophyllum Guett., Hist. Acad. Sci. Paris Mém. 1754. TYPE: *Cacalia porophyllum* L. = *Porophyllum ruderale* (Jacq.) Cass.

Kleinia Jacq., Enum. Pl. Carib. 8. 1760, not *Kleinia* L. 1753. TYPE: *K. ruderalis* Jacq.
Hunteria Moc. & Ses. ex DC., Prodr. 5: 648. 1836, pro syn.

Glabrous or pubescent, often strong-scented, annual or perennial *herbs* or *shrubs*; stems terete or weakly angled, leafy, erect. *Leaves* alternate or opposite, simple, sessile or petiolate; blades linear to ovate, variously punctate with oil glands. *Inflorescence* cymose, corymbiform, paniculiform, the heads solitary or few at ends of branches, pedunculate. *Heads* discoid; involucres cylindric to campanulate, the bracts uniseriate, 5–9, narrow, free or basally fused, variously punctate with oil glands; receptacle flat or slightly convex, naked; florets all

perfect and fertile, the corollas whitish, yellowish, greenish or purplish, short- to long-tubular, the throat very short to longer than the tube, equally to somewhat unequally 5-lobed, the anthers rounded to weakly sagittate, the appendages short, rhombic or triangular-acute, the style branches long, slender, hirtellous. *Achenes* cylindric or narrowly obpyramidal, striate, variously pubescent; pappus of numerous slender, scabrid bristles. Chromosome base numbers $x = 11, 12, 15$.

Porophyllum, a genus of about 28 species, is widespread in the warmer areas of both North and South America. Several of the species have highly disagreeable odors. In Panama, *Porophyllum* is represented by a single species, *P. ruderale*.

The systematics of *Porophyllum* have been studied recently by Johnson (1969). A useful earlier reference is the one by Rydberg (1916).

Literature:

Johnson, R. R. 1969. Monograph of the plant genus *Porophyllum* (Compositae: Helenieae). Univ. Kansas Sci. Bull. 48: 225–267.

Keil, D. J. & T. F. Stuessy. 1975. Chromosome counts of Compositae from the United States, Mexico and Guatemala. Rhodora 77: 171–195.

1. **Porophyllum ruderale** (Jacq.) Cass., Dict. Sci. Nat. 43: 53. 1826.

Stout, malodorous, tap-rooted, annual *herbs*; stems erect, 0.15–1.5 m tall, often much branched above, terete, striate, leafy, green or purplish, often glaucous, glabrous. *Leaves* opposite or alternate, slender-petiolate, simple, ovate, elliptical or obovate, cuneate, crisped-undulate or crenate, pinnately veined, glabrous, often glaucous, punctate with conspicuous, crescent-shaped or oblong marginal oil glands and sometimes with additional scattered glands. *Inflorescence* corymbiform; peduncles 3–5 cm long, terminating leafy branches, glabrous, often glaucous. *Heads* discoid; involucres cylindric at anthesis, 13–22 mm long, 5–10 mm diam., the bracts 5, linear-oblong, acute, flat, glabrous, glaucous, streaked with elongate glands, the margin thin, hyaline; florets 30–60, the corollas greenish to purplish, 10–13 mm long, sparsely puberulent, the tube slender, 8–10 mm long, the throat short, abruptly expanded, equally 5-lobed, the anthers 1.5–2 mm long with short acute to acuminate, rhombic appendages, the style branches long, slender, curved. *Achenes* cylindric, black or brownish, densely hispidulous, 7–12 mm long; carpopodium conspicuous; pappus of many slender, scabrid, tawny bristles 7–11 mm long.

The range of *Porophyllum ruderale* nearly equals that of the genus, extending from the southwestern United States and the West Indies south to northern Argentina. Two widespread varieties occur within this broad range, both of which are found in Panama. According to Johnson (1969), intermediates between the two varieties occur in northern South America, but such intermediates are unknown in Panama.

a. Leaf blades mostly 2–9 cm long; peduncles not or only slightly inflated ---------- 1a. *P. ruderale* var. *ruderale*

aa. Leaf blades mostly 1–2.5 cm long; peduncles strongly inflated ---------- 1b. *P. ruderale* var. *macrocephalum*

1a. **Porophyllum ruderale** var. **ruderale**.

Cacalia porophyllum L., Sp. Pl. 834. 1753. TYPE: Herb. Linn. 976.8 or 976.9 (LINN, not seen).
Kleinia ruderalis Jacq., Enum. Pl. Carib. 28. 1760. LECTOTYPE (here designated): Jacq., Sel. Stirp. Amer. *tab. 127*. 1763.
Cacalia ruderalis (Jacq.) Swartz, Prodr. Veg. Ind. Occ. 110. 1788.
C. glandulosa Salisb., Prodr. 187. 1796, based on *C. porophyllum* L.
Kleinia porophyllum (L.) Willd., Sp. Pl. 3: 1738. 1804.
Porophyllum ellipticum Cass. Dict. Sci. Nat. 43: 56. 1826, based on *Cacalia porophyllum* L.
P. ellipticum Cass. *β intermedium* DC., Prodr. 5: 648. 1836. SYNTYPES: Brazil, Rio de Janeiro, 1834, *Gaudichaud 680* (G-DC, not seen, IDC Microfiche 800. 970: I. 7b). *Gaudichaud s.n.* (G-DC, not seen, IDC Microfiche 800. 970: I. 8). Brazil, Sierra los Orgãos (Province de Rio de Janeiro), 1833, *Vauthier 305* (G-DC, not seen, IDC Microfiche 800. 970: I. 7a). Brazil, Bahia, 1832, *Blanchet* (G-DC, not seen, IDC Microfiche 800. 970: I. 6).
P. latefolium Benth., Jour. Bot. (Hooker) 2: 44. 1840. pro parte (fide Johnson, 1969). TYPE: Guiana, "Dry savannas on the upper Rupunoony," *Schomburgk 442* (K, holotype, not seen).
P. porophyllum (L.) Kuntze, Rev. Gen. Pl. 3: 168. 1898, nom. illeg.
P. macrolepidium Malme, Kongl. Svenska Vetenskapsakad. Handl. 32: 69. 1899. TYPE: Brazil, Mato Grosso, Cuyaba, 7 Feb. 1894, *Malme 1368B* (not seen).
P. ellipticum var. *genuinum* Urb., Symb. Antil. 1: 467, 1900, nom. illeg.
P. ellipticum var. *ruderale* (Jacq.) Urb., Symb. Antil. 1: 468. 1900.
P. ruderale var. *macrolepidium* (Malme) Chodat, Bull. Herb. Boissier, sér. 2, 3: 729. 1903.
P. ruderale f. *suffruticosa* Chodat, Bull. Herb. Boissier, sér. 2, 3: 729. 1903. TYPE: Paraguay, "ad marginem silvae in regione fluminis Apa, Nov.," *Hassler 7995b* (not seen).
P. ruderale var. *glandulosum* Chodat, Bull. Herb. Boissier, sér. 2, 3: 729. 1903. TYPE: Paraguay, "in campis pr. Vaqueria Capibary, Sep.," *Hassler 4495* (not seen).
P. ruderale var. *angustifolia* Hassler, Trab. Mus. Farm. Fac. Ci. Med. Buenos Aires 21: 131. 1909. SYNTYPES: Argentina, "campos y orillas de los montes, flor mayo y agosta," *Rojas 128, 596* (not seen).
Tagetes integrifolia Musch., Bot. Jahrb. Syst. (50 Beibl.) 111: 77. 1913. SYNTYPES: Peru, "supra San Bartolome," 27 Mar. 1910, *Weberbauer 5259, 5260* (not seen). Peru, "prope Cocachacra," 27 Mar. 1910, *Weberbauer 5263* (not seen).
Porophyllum ruderale var. *ellipticum* (Cass.) A. Gray ex B. L. Robinson, Proc. Amer. Acad. Arts 49: 509. 1913.

Herbs 0.3–1.5 m tall. *Leaves* with blades 1–9 cm long, 0.6–5.5 cm broad; petioles 0.8–4 cm long. *Inflorescence* with peduncles 3–5 cm long, weakly if at all clavate. *Heads* with involucres 13–20 mm long, 5–7 mm diam., the bracts streaked with 2 vertical rows of elongate oil glands; florets 30–50, the corollas 10–13 mm long, the tube 8–10 mm long, the lobes ca. 1 mm long, the anthers 1.5 mm long. *Achenes* 7–9 mm long; carpopodium 0.3 mm long; pappus 7–11 mm long. Chromosome number $n = 11, 22$ (Johnson, 1969).

Porophyllum ruderale var. *ruderale* ranges from Costa Rica to Argentina and is also found on several Caribbean islands. Variety *ruderale* is more common in Panama than var. *macrocephalum*, occurring in a range of elevations in Los Santos, Panamá and Darién Provinces and also in the Canal Zone. This variety is rather weedy but it does not become a nuisance in cultivated areas. It flowers the year round.

CANAL ZONE: Fort Clayton, 2600 ft, *Blum et al. 1830* (FSU). Ancón, *Celestine 19* (US). Gamboa, *Greenman & Greenman 5162* (MO). Mouth of Río Chagres, *Piper 5927* (US). Balboa, *Standley 25624, 30888* (both US). Sosa Hill, Balboa, *Standley 26460* (US). Vic. of Fort Sherman, *Standley 31217* (GH, US). Between France Field and Cativa1, *Standley 30365* (US). DARIÉN: Quebrada Nigua below Santa Fe, *Duke 8823* (DUKE, MO). Tres Bocas on Río Cuasí, *Kirkbride & Duke 1360* (US). 2 mi E of Santa Fe, *Tyson et al. 4822* (MO). LOS SANTOS: 1–10 mi S of Tonosí, *Duke 12490* (MO). 17.8 mi S of Macaracas, 1100 ft, *Lewis et al. 1617* (MO). PANAMÁ: 5–6 mi E of Chepo, *Duke 4042* (GH, MO). Halfway between El Llano

and Río Mamoní, *Duke 5607* (GH, MO). Tocumen, *Dwyer 4409* (FSU), *5126* (MO). Río Tapía, *Standley 28114* (US). Juan Díaz, *Standley 30632* (US). Cañita, 18 mi E of Chepo, *Tyson & Smith 4127* (FSU, MO).

1b. **Porophyllum ruderale** var. **macrocephalum** (DC.) Cronq., Madroño 20: 255. 1970.—Fig. 92.

P. macrocephalum DC., Prodr. 5: 648. 1836. TYPE: Mexico, "prope Villalpando," *Mendez s.n.* (G-DC, holotype, not seen, F, photo).
Kleinia glandulosa Moc. & Ses. ex DC., Prodr. 5: 648. 1836, pro. syn.
Porophyllum latefolium Benth., Jour. Bot. (Hooker) 2: 44. 1840, (*fide* Johnson, 1969). TYPE: Guiana, "dry savannas on the upper Rupunoony," *Schomburgk 442*, pro parte (holotype probably at K, not seen).
P. ruderale subsp. *macrocephalum* (DC.) R. R. Johnson, Univ. Kansas Sci. Bull. 48: 233. 1969.

Herbs 0.15–1.25 m tall. *Leaves* with blades 7–25 mm long, 4–13 mm wide; petioles 5–15 mm long. *Inflorescences* with peduncles 3–4 cm long, strongly clavate-inflated. *Heads* with involucres 20–22 mm long, 6–10 mm diameter, the bracts streaked with 2–3 vertical rows of elongate oil glands; florets 40–60, the corollas 10–12 mm long, the tube 8–9 mm long, the lobes 1–1.5 mm long, the anthers 1.5–2 mm long. *Achenes* 11–12 mm long; carpopodium 0.5–1 mm long; pappus 7–9 mm long. *Chromosome number* $n = 11$ (Johnson, 1969; Keil & Stuessy, 1975).

Porophyllum ruderale var. *macrocephalum* occurs from Arizona and Texas south through Mexico and Central America and in South America from Colombia to Bolivia. The odor of the plants of this variety is particularly unpleasant. In Panama, var. *macrocephalum* is uncommon and is known only from a few sites in Coclé Province and the Canal Zone. It flowers from December to March.

CANAL ZONE: Cocoli, *Dwyer 7208* (GH, MO). Cocoli Road, *Lewis et al. 775* (F, GH, MO, UC). COCLÉ: Río Hato Airstrip, *Burch et al. 1153* (MO). Between Porto Portada and Penonomé, 50–1000 ft, *Williams 169* (NY, US).

92. TAGETES

Tagetes L., Sp. Pl. 887. 1753. TYPE: *T. patula* L.

Diglossus Cass., Bull. Soc. Philom. 1817: 70. 1817. TYPE: *D. variabilis* Cass.
Enalcida Cass., Bull. Soc. Philom. 1819: 31. 1819. LECTOTYPE: *E. pilifera* Cass.
Solenotheca Nutt., Trans. Amer. Philos. Soc., n.s. 7: 371. 1841. TYPE: *S. tenella* Nutt.

Annual or perennial *herbs*, glabrous or pubescent, usually strong-scented; stems slender or stout, leafy, often much branched. *Leaves* opposite below, opposite or alternate above, simple and entire to deeply pinnatifid, or pinnately compound, the margins entire to serrate, glabrous or pubescent, variously gland-dotted. *Inflorescence* cymose or the heads solitary; peduncles short to elongate, slender to markedly inflated. *Heads* radiate or rarely discoid, small to large; involucres cylindric, fusiform or campanulate, the bracts uniseriate, marginally fused nearly to the tips, variously punctate; receptacles flat to convex, naked; ray florets fertile, few to many, the ligules small to large, white, yellow, or orange, sometimes spotted with brown, the tube slender, the style branches slender; disc florets perfect and fertile, few to many, the corollas yellow or orange, equally or unequally 4–5-lobed, the anthers weakly sagittate basally, the appendages

D.K.
A
B
C
D.K.
D.K.

triangular-acute, the style branches long, slender. *Achenes* elongate, slender, several-angled, variously pubescent; carpopodium short; pappus of pales and/or scales. Chromosome base numbers $x = 11, 12$ (Towner, 1961; Strother, 1969).

Tagetes, a genus of about 40 species, includes several familiar ornamentals, the garden marigolds. In addition to these cultivated species, wild taxa of the genus occur from the southwestern United States to northern Argentina. In Panama, the genus is represented by one cultivated species, *T. erecta*, the common "French" marigold, and two native species, *T. filifolia* and *T. microglossa*.

No published revision for the entire genus exists. Rydberg (1915) treated the genus for North America. In preparation of the present treatment, an unpublished source (Neher, 1963), has proven useful.

Literature:

Neher, R. T. 1963. Monograph of the genus *Tagetes* (Compositae). Ph.D. thesis, Indiana University.

———. 1967. *In* Documented chromosome numbers of plants. Madroño 19: 134–136.

Towner, J. W. 1961. Cytogenetic studies on the origin of *Tagetes patula*. Meiosis and morphology of diploid and allotetraploid *T. erecta* × *T. tenuifolia*. Amer. Jour. Bot. 48: 743–751.

a. Leaf divisions linear-lanceolate, serrate; ray florets yellow.
  b. Involucres cylindric; rays 3–5 ..... 3. *T. microglossa*
  bb. Involucres broadly campanulate; rays 8–many ..... 1. *T. erecta*
aa. Leaf divisions linear, entire; ray florets (when present) white ..... 2. *T. filifolia*

1. **Tagetes erecta** L., Sp. Pl. 887. 1753. TYPE: not seen.

T. major Gaertn., Fruct. 2: 437. 1791. TYPE: not seen.

Stout, strong-scented, fibrous-rooted, annual *herbs*; stems erect, 0.3–1 m tall, very leafy, much branched above, ribbed, glabrous or puberulent to villous in lines. *Leaves* opposite below, alternate above, 5–20 cm long, odd-pinnate with a narrowly winged rachis, the leaflets opposite or alternate, lanceolate, acute to acuminate, sharply serrate to subentire, the lowermost reduced in size and often setiform-dissected, glabrous or puberulent near the base, punctate with circular oil glands in submarginal rows. *Inflorescence* of a few terminal solitary heads; peduncles 5–15 cm long, with several setiform-dissected bracts near the base, naked and strongly clavate-inflated above, glabrous, often glaucous. *Heads* radiate, often double, showy; involucres campanulate, 13–19 mm high, 9–25 mm broad, the bracts 7–11, marginally fused nearly to the short erect triangular tips, sometimes splitting apart in age, glabrous, glaucous, punctate in two submarginal vertical rows with elliptical oil glands, the free tips with 2–7 ovate glands; ray florets few (8–10) or in double forms very numerous and grading into the disc

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FIGURE 92. *Porophyllum ruderale* var. *macrocephalum* (DC.) Cronq.—A. Habit (× 3/5).—B. Corolla (× 2 4/5).—C. Achene (× 2 4/5). [After *Lewis et al.* 775 (MO).]

florets, the corollas yellow, 10–20 mm long, the tube slender, the ligule broad, showy, entire to deeply cleft; disc florets 100–200, the corollas yellow, equally to very unequally 4–5-lobed, sometimes ciliate-margined or pubescent within, the anthers 2–3 mm long with short triangular appendages, the style branches elongate, slender. *Achenes* 6.5–9 mm long, black, angled, minutely pubescent on the angles or glabrous, narrowed to a shiny knoblike carpopodium; pappus of 1 or 2 stout, long-acuminate, flattened bristles 8–11 mm long and 2–3 more-or-less united truncate scales or bristles 3–6 mm long. Chromosome numbers $n = 12$ (24) (Towner, 1961).

Tagetes erecta, the horticultural "French" marigold, is probably native to Mexico where it was under cultivation prior to the Spanish conquest. It is doubtful whether any extant populations of *T. erecta* actually represent the "wild" form of this species. The "French" marigold is extremely variable and comprises many cultivars. The double forms of *T. erecta*, some of which are grown in Panama, are extremely variable in size and shape of the corollas.

In Panama, *Tagetes erecta* is commonly cultivated and frequently escapes into fields and along roadsides. It flowers the year round, at least in cultivation. The plants are used medicinally in some areas because the strongly scented essential oils are assumed to have some healing properties. Additionally, the marigold is used in much of Latin America in connection with religious ceremonies. The use of this plant in the celebration of All Saints Day has resulted in the common name, "Flor de Muerto" (Neher, 1963).

BOCAS DEL TORO: Isla Colón, vic. of Chiriquí Lagoon, *von Wedel 2832* (GH, MO, US). CANAL ZONE: Summit Garden, *Croat 10285* (MO). Río Pedro Miguel, near El Paraíso, *Standley 30007* (US). CHIRIQUÍ: Boquete, *Ebinger 659* (F, MO, US). COCLÉ: 10 mi E of Río Hato, *D'Arcy 6275* (MO). PANAMÁ: Taboga Island, *D'Arcy 6808* (MO). Sabanas, *Paul 37* (US). Río Tapía, *Standley 28164* (US). Juan Díaz, *Standley 30522* (US).

2. **Tagetes filifolia** Lag., Elench. Pl. 28. 1816. TYPE: Cultivated at the Royal Botanic Garden of Madrid from seed sent from Mexico by Sessé and Mociño (?MA, not seen).—FIG. 93F–J.

Diglossus variabilis Cass., Dict. Sci. Nat. 13: 241. 1819. TYPE: not seen.
Tagetes pusilla H.B.K., Nov. Gen. Sp. Pl. 4: 194. 1820(1818). TYPE: Ecuador, "prope Chillo Quitensium," *Humboldt & Bonpland s.n.* (P, holotype, not seen, IDC microfiche 6209. 107: I. 2; B, isotype, if extant, not seen, F, photo).
T. foeniculacea Poepp. ex DC., Prodr. 5: 646. 1836, not *T. foeniculacea* Desf. 1829. TYPE: Peru, *Poeppig 26* (G-DC, holotype, not seen, F, photo; NY, isotype, not seen).
T. multifida DC., Prodr. 5: 646. 1836. TYPE: Mexico, "ad Lerma," *Berlandier 1145* (G-DC, holotype, not seen, F, photo).
T. pauciloba DC., Prodr. 5: 644. 1836. TYPE: not seen.
T. silenoides Meyen & Walp., Nov. Actorum Acad. Caes. Leop.-Carol. Nat. Cur. 19. Suppl. 1: 272. 1843. TYPE: Peru, Lago de Titicaca, *Meyen s.n.* (B, holotype, probably destroyed, F, photo).
T. dichotomum Turcz., Bull. Soc. Imp. Naturalistes Moscou 24: 72. 1851. TYPE: Ecuador, "prope Quito," *Jameson 865* (G, isotype, not seen, F, photo).
T. scabra Brandegee, Zoe 1: 314. 1890. TYPE: Guatemala, Antigua, collector not known, (UC, holotype, not seen).
T. anisata Lillo in Zelada, Invest. Indust. Publ. Univ. Tucuman 8: 3. 1918. TYPE: Argentina, San Javier, Villa Nougues, *Nougues s.n.* (LIL, holotype, not seen).

Bushy, anise-scented, annual *herbs* 10–30 cm tall; stems glabrous, slender, green to purplish, striate, much branched. *Leaves* opposite, or alternate above, short-petioled, pinnately dissected, 1–2 cm long, the lobes linear, 1–8 mm long, 0.2–0.5 mm wide, mucronate to aristate, the lowermost usually reduced to slender bristly cilia, marginally scabrid to glabrescent, densely punctate on the undersurface with tiny round translucent oil glands. *Inflorescence* of leafy bracted cymes; peduncles slender, 1–20 mm long. *Heads* radiate or discoid; involucre ellipsoid to cylindric, 2–3 mm diam., the bracts 5, linear to narrowly elliptic, 6–7 mm long, marginally connate nearly to the abruptly short-aristate tips, several-nerved, more-or-less indurate-keeled below, glabrous, densely punctate in irregular lines with tiny round, translucent oil glands; receptacle short-conic, pitted; ray florets 0–2, inconspicuous, white to pale yellow, the tube slender, glabrous or minutely puberulent, 1–2 mm long, the ligules ovate, ca. 1 mm long; disc florets 5–10, the corollas pale yellow, slender, 3–4 mm long, glabrous, the lobes slender, 0.5–1 mm long, the anthers 0.5 mm long, tapering to short, acute appendages, the style branches ca. 0.5 mm long, included or scarcely exserted. *Achenes* 3–4.5 mm long, black or brown, linear to narrowly turbinate, strigillose; carpopodium short, knoblike; pappus of 2–3 stiff, scale-based bristles 3–4 mm long and 2 lacerate-margined scales 1–2 mm long. Chromosome number $n = 12$ (Neher, 1967).

Tagetes filifolia is the most widespread species of the genus, extending from the highlands of northern Mexico south along the mountains to northern Argentina. This species has a very restricted distribution in Panama, occurring only above 1,000 m in the mountains of western Chiriquí. It flowers from December to May.

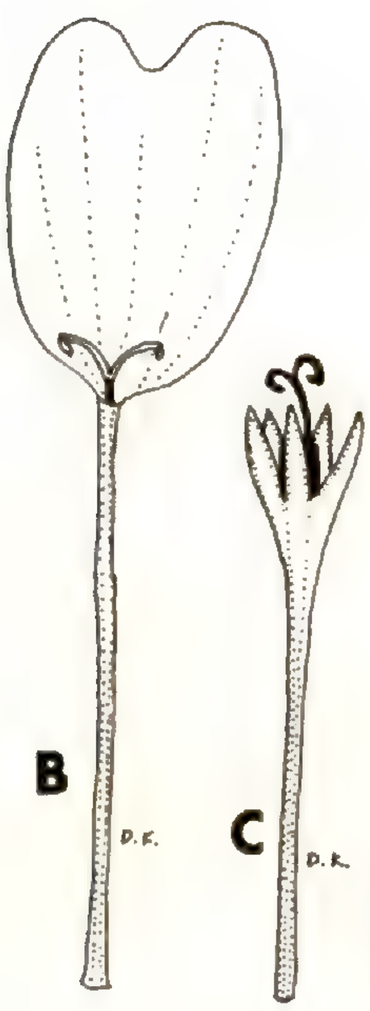
The sweet anise scent of the essential oils of *T. filifolia* is the basis of one of the colloquial names, "Anisillo." The plants are sometimes used to prepare a medicinal tea. This species, like its larger relatives, *T. microglossa* and *T. erecta*, is sometimes known as "Flor de Muerto."

CHIRIQUÍ: 5 km NW del Hato de Volcán, *Correa 1360* (MO). Nueva California, *D'Arcy 4260* (MO). Near Volcán, 4600 ft, *Duke 9161* (MO, OS), *9201* (MO). Vic. of Boquete, 3300–4200 ft, *Lewis et al. 357* (GH, MO). Around Alto Lino, 4200 ft, *Maurice 863* (US). 1.5 mi NE of El Hato de Volcán, 1500 m, *McDaniel 10186* (FSU). Cerro Vaca, 900–1136 m, *Pittier 5341* (US). 5 mi NE of El Hato de Volcán, *Wilbur et al. 11863* (DUKE). ½ mi from Hato de Volcán, *Wilbur et al. 11949* (DUKE). 2.5 mi W of El Hato de Volcán, *Wilbur et al. 15101* (DUKE).

3. **Tagetes microglossa** Benth., Bot. Voy. Sulphur 118. 1845. TYPE: Ecuador, near Salango, *462* (BM, holotype, not seen).—FIG. 93A–E.

T. macroglossa Polak., Linnaea 41:580. 1877. TYPE: Costa Rica, "ad vias prope San José," 29 Nov. 1875, *Polakowski 372* (B?, holotype, not seen, F, photo).

Stout, strong-scented, erect, fibrous-rooted, annual *herbs*; stems 0.3–1 m tall, leafy, ribbed, glabrous or puberulent in lines, often purplish. *Leaves* opposite below, usually alternate above, 3–7 cm long, odd-pinnate, with a narrowly winged rachis, the leaflets linear to lanceolate, 1–2 cm long, acute to acuminate, serrate, the lowermost leaflets and those of the uppermost leaves reduced in size and setiform-dissected, glabrous, punctate with submarginal rows of circular oil glands,



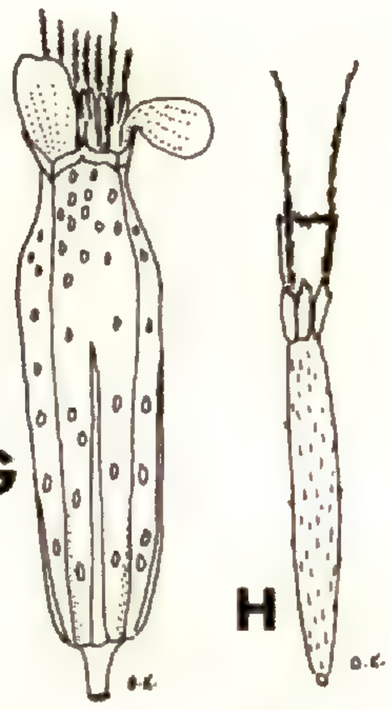


Figure 93. *Tagetes*.—A–E. *T. microglossa* Benth.—A. Habit (× ½).—B. Ray corolla (× 4½).—C. Disc corolla (× 4½).—D. Achene (× 2⅜10).—E. Head (× 2⅜10). [After *White & White 114* (MO).]—F–J. *T. filifolia* Lag.—F. Habit (× ½).—G. Head (× 4½).—H. Achene (× 4½).—I. Disc corolla (× 9).—J. Ray corolla (× 9). [After *Lewis et al.* 357 (MO).]

sometimes with additional glands scattered on the undersurface. *Inflorescence* an open corymbiform cluster; peduncles 2–3 cm long, with one or more setiform-lacerate bracts below, slightly clavate above, glabrous. *Heads* radiate; involucres cylindrical or slightly fusiform, 15–20 mm long, 4–7 mm wide, the bracts 5, fused nearly to the triangular-acute spreading tips, often splitting apart in age, glabrous, punctate in submarginal rows with 3–6 linear to elliptic glands and 1 or 2 oval, subterminal glands; ray florets 3–5, inconspicuous, the corollas yellow, the tube slender, glabrous, 6–7 mm long, the ligule narrow to ovate, erect or spreading, about ½ the length of the tube, sometimes essentially absent, the style branches slender, curled, shorter than to exceeding the ligules; disc florets 20–25, the corollas yellow, slender, 8–9.5 mm long, equally 5-lobed, the tube scarcely differentiated from the throat, the anthers included, ca. 2 mm long, with elongate, deltoid appendages, the style branches elongate, curved, with a scarcely discernable appendage. *Achenes* 4-angled, black, clavate, 8 mm long, strigillose on the angles, otherwise glabrous; carpopodium short, knoblike; pappus of 2 stout, elongate, upwardly scabrous, acuminate bristles 8–9 mm long, and 1 broad, erose-truncate scale 3–4 mm long.

Tagetes microglossa occurs throughout much of Central America and extends south into Colombia and Ecuador. In Panama, this species occurs only in the mountains of Chiriquí and Veraguas at elevations above 1,000 m. The one collection from Veraguas is unusual in having extremely tiny ligules, almost completely concealed by the pappus. It flowers from December to April.

Like its more conspicuous relative, *Tagetes erecta*, *T. microglossa* is sometimes used in religious ceremonies or for medicinal purposes. This species is known by several colloquial names in Panama: "Flor de Muerto," "Rudillo" and "Manzanilla." The odor of the essential oils and the vegetative morphology of *T. microglossa* are very similar to those of *T. erecta*.

CHIRIQUÍ: 5.4 km del Hato de Volcán, *Correa & Lazor 1473* (DUKE, MO). Between Bajo and Alto Lino, 4000 ft, *Maurice 895* (US). Cerro Vaca, 900–1133 m, *Pittier 5306* (US). NE of Cerro Pando, NW of Nueva California, 1500 m, *Wilbur et al. 11008* (DUKE). Valley of upper Río Chiriquí Viejo, *White & White 114* (MO). VERAGUAS: 1–2 mi above Santa Fe, *Gentry 3069* (MO).

VII. ANTHEMIDEAE

W. G. D'ARCY[58]

Anthemideae Cass., Jour. Phys. 88: 192. 1819. TYPE: *Anthemis* L.

Aromatic *shrubs* or *herbs*. *Leaves* mostly alternate, often dissected; hairs often arachnoid. *Heads* radiate (Panama), discoid or disciform; involucre of 2–many bracts in several series, imbricate, often with scarious or hyaline margins;

[58] Missouri Botanical Garden, 2315 Tower Grove Avenue, St. Louis, Missouri 63110.

receptacle flat or convex; paleas mostly wanting; ligules entire or 1–3-denticulate; corolla of disc florets mostly yellowish, tubular, 4–5-dentate, the anthers obtuse, appendaged, the style branches mostly truncate. *Achene* mostly small; pappus mostly wanting.

The Anthemideae is a large tribe of extratropical regions with many species in both hemispheres and in Australia. The few species known to tropical America are restricted to upper elevations or, as in Panama, are escapes from horticultural introductions.

93. CHRYSANTHEMUM

Chrysanthemum L., Sp. Pl. 887. 1753; Gen. Pl., ed. 5. 379. 1754. TYPE: *C. coronarium* L.

Leucanthemum Lam., Fl. Françoise 2: 136. 1778. TYPE: *L. vulgare* L.

Mostly erect and branched annual or perennial *herbs*, rarely *shrubs*, often strong scented. *Leaves* alternate, entire to much dissected, glabrate or sometimes pubescent. *Inflorescence* of solitary heads or paniculate, cymose or solitary, the heads long stalked. *Heads* mostly conspicuously radiate, rarely discoid, with many florets, variously colored, often showy; involucral bracts narrow in 3–4 similar but unequal series, the costa darkened with a hyaline, often brownish margin, at least at the tips; receptacle flat or convex; paleas present or not; ray florets in one or many series, the ligule entire or dentate, the tube terete, flattened or rarely winged, larger at the base, the ovary mostly fertile; disc florets numerous, the corolla mostly yellowish with little distinction between tube and limb, apically (4–)5-dentate, the anthers basally obtuse or truncate, apically appendaged, the style sometimes basally enlarged, the branches with a ventral groove and flat and fringed at the truncate, sometimes expanded apex, the ovary mostly like that of the ray floret but less compressed, or sometimes shrivelled and sterile. *Achene* mostly dorsiventrally flattened, sometimes 3-angled or winged, mostly with 5–10 prominent regular sulci or nerves; carpopodium inconspicuous; pappus wanting or an interrupted ring of scales.

Chrysanthemum is sometimes interpreted narrowly to include about 5 species of Europe and the Mediterranean region, or sometimes broadly to include over 200 species widely dispersed in the Old World. In Panama, the genus is distinct in its aromatic foliage, broad rays, and achenes with conspicuous, evenly spaced nerves or sulci. It is known here only by two cultivated and sometimes escaping Old World species.

Plants in this genus are mostly aromatic and have been used in folk medicine in a number of countries. Contact with the leaves may cause dermatitis. Two species (not in Panama) are used for insecticides known as pyrethrins or Dalmation powder.

a. Heads more than 25 mm across; leaves of the stem remotely denticulate, eglandular beneath; plants mostly exceeding 70 cm tall; scaly pappus well developed ---------- 1. *C. leucanthemum*

aa. Heads less than 20 mm across; leaves of the stem saliently toothed, copiously glandular beneath; plants seldom exceeding 60 cm tall; pappus rudimentary (scaly) or wanting .... 2. *C. parthenium*

1. **Chrysanthemum leucanthemum** L., Sp. Pl. 888. 1753. TYPE: not seen.

Leucanthemum vulgare Lam., Fl. Françoise 2: 137. 1778. Based on *Chrysanthemum leucanthemum* L.

Glabrate, branched, aromatic perennial *herb* to 1 m tall, densely leafy; stems soft, stout, glabrous, slightly striate. Basal *leaves* spatulate, to 15 cm long, the lower half narrowed into a slender winged petiole, prominently serrate upwards, callose margined; cauline leaves lanceolate, to 10 cm long, remotely denticulate or entire, sessile and somewhat clasping at the base, callose margined, glabrous or apically sparingly pubescent. *Heads* radiate, showy, solitary, 5–9 cm across with white ray and yellow disc florets, sometimes with one or two slender subinvolucral bracts; involucral bracts herbaceous in ca. 3 imbricate series, narrowly deltoid to oblong, ca. 10 mm long with broad, brownish, erose, hyaline margins, glabrous; receptacle convex; ray florets 20–30 in apparently 1 series, ligules 3 cm long, 5 mm broad, apically denticulate, drying with longitudinal brown lines, the tube 1–2 mm long, the style white, included, the branches colored, exserted, with a prominent, ventral groove and an expanded, truncate, flat, short-fringed apex, the ovary ca. 2 mm long, glabrous, dorsiventrally flattened, deeply 10-sulcate, the pappus an interrupted ring of scales; disc florets numerous, ca. 6 mm long, the corolla not differentiated into tube and limb, 4 mm long, obconical, apically 5-dentate, the anthers 2 mm long, basally truncate, the appendages obtuse or deltoid, the ovary 2 mm long, resembling that of the ray florets but less compressed, the style branches like those of the ray florets but the apical fringe much larger. *Achene* black, compressed, with conspicuously contrasting ribs, glabrous; pappus of irregular scales or wanting.

This species is distinguished by its large showy flowers and aromatic foliage. It is grown for ornament in upland Chiriquí and sometimes offered for sale as cut flowers in lowland markets. It is a native of the Old World. "Marguarita."

CHIRIQUÍ: Nursery in Boquete, *D'Arcy & D'Arcy 6506* (MO), *6508* (K, MO, PMA).

2. **Chrysanthemum parthenium** (L.) Bernh., Syst. Verz. Erfurt 145. 1800.

Matricaria parthenium L., Sp. Pl. 890. 1753. TYPE: not seen.

Puberulent, branched, aromatic *herb* to 60 cm tall; stems densely leafy, prominently angled, puberulent. *Leaves* to 5 cm long, elliptic or obovate, bipinnately dissected, ultimately obtuse, mucronate, membranaceous, minutely puberulent; base narrowed into a slender, winged petiole 1–2 cm long. *Inflorescence* an open, several–many-flowered panicle; pedicels stout, 3–8 cm long, puberulent, with scalelike bracts along their length. *Heads* small but showy, 15–20 mm across; involucral bracts herbaceous in about 3 unequal, imbricate series, lanceolate, ca. 3 mm long, stramineous, the midvein drying dark and apically pilose, glandular beneath; paleas present; ray florets with ligules 5 mm long, 3 mm broad, apically 3-lobed, the tube 1 mm long, strongly dorsiventrally

compressed, enlarged near the base, the ovary glabrous, dorsiventrally flattened and curving inwards, obconical with 5 prominent nerves; disc florets 3.5 mm long, the corolla yellow, not clearly differentiated into tube and limb, straight or arcuate, mostly tubular, the anthers 1 mm long, basally obtuse, the appendages elongate-obtuse, the style basally enlarged, the branches with a prominent ventral groove and expanded, truncate, flat, fringed apex, the ovary sterile, shrivelled. *Achene* ca. 1.3 mm long; pappus wanting or a short, erose, fringe of scales. *Pollen* brilliant yellow.

This species somewhat resembles species of *Erigeron* but has much broader rays and a hemispherical mass of disc florets. It is grown for ornament in upland Chiriquí. Native of Europe, it is cultivated and escapes in many countries, the oil formerly finding use as a febrifuge. "Feverfew" (English), "Manzanilla" (Panama).

CHIRIQUÍ: Boquete, 5500 ft, *Dwyer 7014* (MO).

VIII. SENECIONEAE[59, 60]

T. M. BARKLEY[61]

Senecioneae Cass., Bull. Soc. Philom. 173. 1815; Dict. Sci. Nat. 20: 377. 1821.

Shrubs, subshrubs or coarse *herbs, lianas,* or short-lived seasonal herbs. *Leaves* alternate, opposite, or mostly basal. *Heads* radiate, disciform, or discoid, florets usually numerous; involucre often of a single series of prominent involucral bracts, sometimes subtended by a series of conspicuously reduced (calyculate) bracts, or the involucre of 3–4 series of imbricate bracts; receptacle usually naked but with paleas in *Neurolaena, Schistocarpha* and 1 species of *Liabum*; ray florets usually distinctly ligulate, the corolla reflexed and prominent but sometimes erect and short, sometimes tubular-filiform and erect; disc florets with the corolla tubular and erect, the anthers appendaged and blunt to slightly tailed at the base, the style branches truncate, terminated with short, spreading hairs (senecionioid style branch) or appendaged with a short, pointed tuft of fused hairs. *Achenes* columnar to narrowly napiform, terete or variously angled, pubescent-hirsute or glabrous; pappus of copious, capillary, smooth or minutely barbellate hairs.

Extensive generic realignments wth the Senecioneae as traditionally conceived have been recently proposed by Robinson and Brettell in a series of papers in *Phytologia.* They include erecting a new tribe, Liabeae, for *Liabum,* and

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[60] I am grateful to Dr. H. Robinson for assistance and advice in the preparation of this treatment and to Rupert Barneby, New York Botanical Garden, for the Latin description of *Senecio angustiradiatus.*

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transferring *Neurolaena* and *Schistocarpha* to the Heliantheae. Their generally narrower generic concept also increases the number of genera. Their work is intriguing and will receive serious consideration, especially because it incorporates detailed observations of floral structures. However, I have elected to follow the traditional circumscription and generic alignments of the tribe for the *Flora of Panama*, because adopting the work of Robinson and Brettell would entail studies beyond the time and resources available, and further because the pertinent structural variation used by Robinson and Brettell occurs in species not found in Panama.

Generic typification follows that of Rydberg (1927).

Literature:

Rydberg, P. A. 1927. (Carduales) Carduaceae. Liabeae, Neurolaeneae, Senecioneae. N. Amer. Fl. 34: 289–360.

a. Involucral bracts in 3–4 series, imbricate.
  b. Leaves opposite; heads radiate or disciform.
    c. Leaves white felted-lanate beneath; style branches apically linear-subulate or filiform ..... 96. *Liabum*
    cc. Leaves green and glabrate beneath; style branches terminated in a tufted crest of hairs ..... 98. *Schistocarpha*
  bb. Leaves alternate: heads discoid ..... 97. *Neurolaena*
aa. Involucral bracts in a single principal series of uniform length, but often subtended by a calyculus of narrow, short, unequal bracteoles.
  d. Plants small seasonal herbs; florets rose-pink, reddish to orange-red, or sometimes white; involucre of a single series of bracts without a calyculus ..... 94. *Emilia*
  dd. Plants without this combination of characters.
    e. Heads disciform; erect, weedy herbs ..... 95. *Erechtites*
    ee. Heads discoid, radiate or disciform in one subsucculent liana; herbs, shrubs, or lianas ..... 99. *Senecio*

94. EMILIA

Emilia Cass., Bull. Soc. Philom. 68. 1817. TYPE: *E. flammea* Cass.

Coarse to frail seasonal weedy *herbs*; taprooted, but with abundant lateral fibrous roots that sometimes overgrow the taproot. *Leaves* alternate, variously petiolate or sessile to distinctly amplexicaul. *Inflorescence* a several-headed, loose-corymbose cyme, arising terminally and sometimes several arising laterally in the axils of the upper leaves. *Heads* discoid, turbinate to weakly campanulate, especially in age; involucral bracts in a single series and equal in length; calyculate bracts absent; receptacle flat or but slightly convex, naked; florets several to numerous, bisexual and fertile, rose to purple or red to orange, occasionally white, the style branches inconspicuously appendaged or surmounted by a short appendage of fused hairs. *Achenes* columnar-rapiform, terete with 10 ribs; pappus of abundant white capillary bristles about equalling the corolla.

An Old World genus of some 24 species, 3 of which are now widely distributed as pan-tropical weeds. The key distinguishes the bulk of specimens of these 3 species that have been seen by me, but the species are imperfectly separated on morphological features and occasional intermediates are to be expected. No specimens referable to *Emilia coccinea* have been seen by me from the Panamanian

flora, however its presence in adjacent regions is undisputed so it may be expected as an occasional weed.

This treatment is adapted from personal communication with F. R. Fosberg, Dan Nicolson, and Arthur Cronquist.

Literature:

Baldwin, J. T., Jr. 1946. Cytogeography of *Emilia* Cass. in the Americas. Bull. Torrey Bot. Club 73: 18–23.

Nicolson, D. H. 1975. *Emilia fosbergii*, a new species. Phytologia 32: 33–34.

a. Involucre about equalling or only slightly shorter than the florets; heads 7–12 mm long, narrow, 3–4 times longer than wide; involucral bracts ca. 8; middle and lower leaves often conspicuously lyrate-lobed; florets lavender-pink to purple or white, less frequently reddish ..... 3. *E. sonchifolia*

aa. Involucre usually at least 2 mm shorter than the florets; heads relatively broad, 3 or less times longer than wide; involucral bracts 8–13; leaves usually dentate or but weakly lobed; florets variously colored, sometimes bright red or orange.

b. Involucral bracts (7–)9–12 mm long, 8–13; heads mostly 2–3 times longer than wide; florets pink to purple or red but not orange ..... 2. *E. fosbergii*

bb. Involucral bracts 6–9 mm long, mostly ca. 13; heads relatively broad, less than 2 times longer than wide; florets often red to orange ..... 1. *E. coccinea*

1. **Emilia coccinea** (Sims) Sweet, Hort. Brit., ed. 3. 382. 1839.

Cacalia sagittata Vahl, Symb. Bot. 3: 91. 1794, nom. illeg., *Hieracium javanicum* N. Burm. (1768) included in synonymy.

C. coccinea Sims, Bot. Mag., *tab. 564.* 1802. TYPE: not seen.

Emilia sagittata (Vahl) DC., Prodr. 6: 302. 1837.

Erect, seasonal *herb*, 1–5 dm tall, glabrous to lightly pilose; taproot present. *Leaves* alternate, the middle and lower cauline leaves ovate to oblanceolate in outline, but variously toothed or lobed to subentire, the teeth callose-tipped, the uppermost leaves reduced to bracts. *Inflorescence* of 1 to several loose, few-headed, corymbiform cymes, arising terminally or laterally in the axils of the upper leaves. *Heads* discoid, urceolate to turbinate, robust, ca. 1½ times longer than wide, the florets prominently exserted to about ½ their length beyond the involucre; involucral bracts ca. 13, linear, 6–9 mm long; receptacle flat to convex; florets with corollas scarlet to red-orange or orange. *Achene* brown to reddish-tan, narrowly rapiform, 3–4 mm long, minutely pubescent along the 10 ribs; pappus of abundant white capillary hairs. Chromosome number $n = 5$.

This is a showy Old World weed, apparently of sporadic occurrence in the New World tropics and subtropics. Not so frequent as either *E. sonchifolia* or *E. fosbergii*, no Panamanian specimens have been seen by me, but it is to be expected in Panama.

2. **Emilia fosbergii** Nicolson, Phytologia 32: 33. 1975. TYPE: Bahamas, *Curtiss 6* (US).—FIG. 94.

E. sagittata sensu auctt., not (Vahl) DC., Prodr. 6: 302. 1837.

E. javanica sensu auctt., not (N. Burm.) C. B. Robinson, Philipp. Jour. Sci. 3: 217. 1908.

Erect to weak seasonal *herb*, (1–)2–5 dm tall, glabrous to sparsely pilose or sometimes prominently villous-pilose in and near the axils of the middle cauline

leaves; taproot present, but becoming branching fibrous-rooted in robust individuals. *Leaves* alternate, broadly ovate to oblanceolate, often tapering to a prominently winged petiole and therefore appearing pandurate, the base sessile to auriculate, the margin weakly serrate to dentate or sometimes lobed, the teeth callose-tipped, overall 5–10 cm long, 2–5 cm wide, about 2 times longer than wide, the uppermost leaves reduced to linear serrate clasping bracts. *Inflorescence* of one to several few-headed, loose, corymbiform cymes arising terminally or laterally in the axils of the upper cauline leaves. *Heads* turbinate or sometimes weakly urceolate or becoming weakly campanulate in age, robust, 2–3 times longer than wide, the florets prominently exserted ca. 2 mm beyond the involucre; involucral bracts 8–13, linear, (7–)9–12 mm long; receptacle flat to convex, the carpopodia forming prominent tubercles after achenes have been shed; florets 15–30, varying greatly in size with the robustness of the plant, the corollas pink to light purple or red but not orange. *Achene* reddish brown to light tan, columnar, ca. 4 mm long with a row of strigose-hirsute pubescence on each of the 5(10) prominent ribs; pappus of abundant, white, capillary hairs. Chromosome number $n = 10$.

This is a common weed at lower elevations. It is native to the Old World but now widely distributed. Less frequent in Panama than the closely related *E. sonchifolia*, *E. fosbergii* is most often collected in flower during August to December.

CANAL ZONE: Road C-21, *Duke 5767* (MO). Balboa, *Standley 27005* (US). Chiva Chiva trail near Mira Flores Lake, *Tyson 1353* (MO). CHIRIQUÍ: 8 mi above David on road to Boquete, *D'Arcy & D'Arcy 6295* (MO). Boquete, *D'Arcy & D'Arcy 6341* (MO). Vic. of Boquete, *Lewis et al. 316* (MO, US). PANAMÁ: Cerro Azul, *Castillo 7* (MO). Beyond Goofy Lake along road to Cerro Jefe, *Correa & Dressler 449* (MO). Cerro Azul, *Croat 17327* (MO). Between Cerro Azul and Cerro Jefe, *D'Arcy & D'Arcy 6223* (MO). Cerro Azul, *Dwyer 2533* (MO); *Tyson 2059, 6323* (both MO).

3. **Emilia sonchifolia** (L.) DC., Prodr. 6: 302. 1837.

Cacalia sonchifolia L., Sp. Pl. 835. 1753.

Erect to weakly spreading *herb*, (10–)30–50 cm tall, mostly glabrous or with sparsely scattered, inconspicuous multicellular hairs; taproot present, but sometimes overgrown by active lateral fibrous roots. *Leaves* alternate, evenly distributed along the stem, the lower and middle cauline leaves ovate to oblanceolate in outline, often tapering to a weakly distinct petiole, the margins crenate to deeply and sharply lyrate-lobed, the lobes callose-tipped, overall 5–12 cm long, 1.5–4.5 cm wide, about 3 times longer than wide, the upper leaves similar and smaller, sessile to amplexicaul, the uppermost reduced to linear, subentire clasping bracts. *Inflorescence* of 1 to several, loose, corymbiform cymes of 4–10 heads, arising terminally or laterally in the axils of the upper leaves. *Heads* discoid, turbinate to weakly campanulate in aging individuals, relatively long and thin, 3–4 times taller than wide, the florets little exserted beyond the involucre; involucral bracts ca. 8, linear, 7–12 mm long, weakly connate along the margins, especially in young heads; receptacle naked, flat or convex, the carpopodia prominent after mature achenes have been shed; florets 10–20, the corolla lavender-pink to light

A
PRA
B
PRA

purple or white, sometimes tinged reddish but not orange, the style branches terminated in a small tuft of hairs of the same color as the corolla. *Achene* brown to reddish brown, columnar to narrowly rapiform, 3–4 mm long, with short white hirsute bristles on the 10 prominent ribs; pappus of abundant white capillary hairs. Chromosome number $n = 5$.

This is a common weed at lower elevations. It is native to the Old World but now widely distributed throughout the tropics and subtropics. Most frequent in habitats created by human disturbance, but also found in gravel bars in stream beds, and similar habitats, it flowers the year round.

BOCAS DEL TORO: above RR stop at mi 7.5, *Croat & Porter 6225* (MO). United Fruit Co., Changuinola Banana Plantation, *Lazor et al. 2442* (MO). Changuinola to 5 mi S at Junction of Ríos Changuinola & Terebe, *Lewis et al. 914* (MO, US). Without definite locality, *von Wedel 328* (MO). CANAL ZONE: Farfan Beach, *Burch et al. 1409* (MO, NY, US). Barro Colorado Island, *Croat 4183* (MO, NY), *6523, 6991, 8488, 9196* (all MO). Halfway between Gamboa and Summit, *Fosberg 27389* (US). Ancón, *Greenman & Greenman 5080* (MO). Gamboa, *Heriberto 15* (US). Frijoles, *King 5229* (US). Ancón, *Macbride & Featherstone 16* (US); *Piper 5816* (US). Between Corozal and Ancón, *Pittier 2207* (US). Barro Colorado Island, *Shattuck 81* (MO). Balboa, *Standley 25657* (US). Near Gatún, *Standley 27320* (US). Gamboa, *Standley 28353* (US). Mt. Hope Cemetery, *Standley 28810* (US). Between France Field and Cativa1, *Standley 30261* (US). Fort Clayton, *Tyson 2788* (MO). CHIRIQUÍ: 2 km N of Punta de Burica, *Busey 754* (MO). 6 mi S of Puerto Armuelles, *Liesner 492* (MO). David airport, *Lewis et al. 763* (MO, US). Vic. of Puerto Armuelles, *Woodson & Schery 844* (MO). COLÓN: Mouth of Río Piedras, *Lewis et al. 3201* (MO). DARIÉN: Vic. of Boca Quebrada Venudo, Río Tuqueza, *Bristan 1092(2)* (MO). HERRERA: Ca. ½ mi E of Río Coroca, *D'Arcy & D'Arcy 6674* (MO). PANAMÁ: Isla Tobaga, *Allen 1275* (MO). Ca. 2 mi from Universidad de Panama, *D'Arcy & D'Arcy 6105* (MO). Pan-Am. Hwy. at Río Mammoní, *Duke 5583* (MO). San José Island, *Erlanson 351* (NY, US). Gorgona Beach, *Woodson et al. 1693* (MO). SAN BLAS: Without definite locality, *Cooper 273* (US).

95. ERECHTITES

Erechtites Raf., Fl. Ludovic. 65. 1817. TYPE: *E. praelta* Raf.

Fibrous rooted, short-lived *herbs*. *Leaves* alternate, petiolate to variously weak-clasping or amplexicaul. *Inflorescences* varying from a single head (in depauperate plants) to many heads in loose to constricted compound cymes. *Heads* disciform; principal involucral bracts in a single series and equal in length, a shorter calyculate series present; receptacle flat to weakly convex, naked; marginal florets in 1–2 series, pistillate, the corolla tubular-filiform; disc florets numerous, fertile, the style branches surmounted by a terminal appendage of fused papillose hairs. *Achenes* terete or inconspicuously ribbed.

Literature:

Belcher, R. O. 1956. A revision of the genus *Erechtites* (Compositae), with inquiries into *Senecio* and *Arrhenechthites*. Ann. Missouri Bot. Gard. 43: 1–85. (This treatment presents an unorthodox generic circumscription but describes the structural and distributional data with admirable precision.)

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FIGURE 94. *Emilia fosbergii* Nicolson—A. Habit (× ½). [After *Tyson & Blum 4055* (MO).]—B. Floret (× 5). [After *Koch 4922*, Costa Rica (MO).]

a. Leaves chiefly sessile, or if short-petiolate, then the petioles clasping; involucral bracts about 2 times longer than the width of the head; pappus white ---------- 1. *E. hieracifolia* var. *cacalioides*

aa. Leaves chiefly petiolate, or if subsessile, then not clasping; involucral bracts about 3 times longer than the width of the head; corollas and pappus usually pink or reddish ---------- 2. *E. valerianaefolia*

1. **Erechtites hieracifolia** (L.) Raf. ex DC., Prodr. 6: 294. 1837.

1a. **Erechtites hieracifolia** var. **cacalioides** (Fisch. ex Spreng.) Griseb., Fl. Brit. W. Ind. 381. 1861.

Senecio cacalioides Fisch. ex Spreng., Novi Prov. Hort. Acad. Hal. 37. 1819.

Short-lived *herb*, 1–3 m tall; glabrous to sparingly pilose or occasionally conspicuously pubescent, especially on young plants; stems simple or branching above, striate. *Leaves* alternate, pinnately veined, sessile or nearly so, often clasping; blades oblong to linear-lanceolate, subentire to variously dentate-sinuate to occasionally subpinnatifid, glabrous, or frequently pilose-pubescent on the undersides, 5–15 cm long, 1–4 cm wide, ca. 4 times longer than wide. *Inflorescence* a terminal and axillary cluster of corymbiform cymes, with 50 or more heads in robust individuals, or a single head in depauperate plants. *Heads* turbinate, disciform, 10–15 cm tall and ca. ½ as wide; principal involucral bracts linear-subulate, in a single series, ca. 21; calyculate bracts linear to filiform, subulate, unequal, ca. ½ as long as the involucral bracts; receptacle flat, naked, and sometimes weakly inflated and fleshy; ray florets in 1 or 2 series, the corollas thin, tubular, filiform; disc florets functional but sometimes not setting seed. *Achenes* turbinate and lightly ribbed, pappus of abundant, soft, white, capillary hairs, protruding 2–5 mm beyond the involucral bracts. Chromosome number $n = 20$.

A weed in disturbed sites, especially agricultural lands, mostly below 800 m, this species flowers the year round but is more frequently collected in July to December.

Belcher (1956) recognizes 3 varieties of *Erechtites hieracifolia*: var. *hieracifolia* with short calyculate bracts, small heads, and an essentially warm-temperate distribution; var. *megalocarpa* (Fernald) Cronq. with short calyculate bracts, large heads, and a distribution restricted to coastal marshes of eastern North America; and var. *cacalioides* (Fisch. ex Spreng.) Griseb. with long calyculate bracts, small heads, and a generally tropical distribution. The varieties *hieracifolia* and *cacalioides* appear to intergrade freely and represent statistical modes in variation rather than morphologically discrete entities.

BOCAS DEL TORO: Almirante, *Blum 1328* (MO). CANAL ZONE: Fort Sherman, *Duke 4359* (MO). Sosa Hill, *Duke 4662* (MO). Gatún, *Hayes 225* (NY). Between Gatún and Piña, *Leisner 1332* (MO). Chiva Chiva trail, Red Tank to Pueblo Nuevo, *Piper 5773* (US). Between Miraflores and Corozal, *Pittier 2197* (US). Barro Colorado Island, *Shattuck 757* (MO). Sosa Hill, *Standley 26417* (US). Gamboa, *Standley 28352* (US). Near Fort Randolph, *Standley 28741* (US). Vic. of Salamanca Hydrographic Station, *Woodson et al. 1611* (NY, US). CHIRIQUÍ: 15.5 km N of Paso Canoas, *Busey 617* (MO). Llanos Francia, 4 mi from Boquete, *Dwyer & Hayden 7605* (MO, US). Vic. of Boquete, *Lewis et al.* 582 (MO, US). 9 mi S of Puerto Armuelles, *Liesner 158* (MO). Around El Boquete, *Pittier 2870, 2906* (both US).

Between Río Tinta and Río Tabasara, *Woodson et al. 418* (MO). COLÓN: Santa Rita Ridge, *D'Arcy & D'Arcy 6173A* (MO). DARIÉN: Vic. of Boca de Cupe, *Allen 903* (MO). Vic. of Santa Fe, Río Sabana, *Duke 4096* (MO). Hill near Río Chucunaque, *Duke 4870* (MO). Teotuma, *Duke 10077(1)* (MO). Manené, *Kirkbride & Bristan 1575* (MO). LOS SANTOS: Los Toretos, *Dwyer 2443A* (US). PANAMÁ: Isla Taboga, *Allen 1270* (MO). Ca. 5 mi N of Chagres River, *Croat & Duncan 15288* (MO). Road N of El Llano, *D'Arcy & D'Arcy 6041* (MO). Along Pan-Am. Hwy., Río Cañita, *Duke 3816* (MO). 6 mi E of Chepo, *Duke 4086* (MO). Río Pacora just below confluence with Río Corzo, *Duke 12028(3)* (MO). Cerro Azul, *Dwyer 1503* (NY); *King 5242* (US). Just E of Chica, *King 5265* (US). Chimán, *Lewis et al. 3293* (MO). Río Tapia, *Standley 28116* (US). Juan Díaz, *Standley 30570* (US). 3 mi E of El Llano at Finca Risso, *Tyson 1733* (MO). Cerro Azul, *Tyson 2106, 6324* (both MO). Cerro Jefe, *Tyson 4305* (MO). Saboga Island, *Tyson & Loftin 5104* (MO). Near Arraiján, *Woodson et al. 1337* (MO, NY). SAN BLAS: Soskatupu, *Elias 1679* (MO). Mainland opposite Achutuppu, *Lewis et al. 133* (MO, US). Mainland opposite Ailigandí, *Lewis et al. 140* (MO). Puerto Obaldía, *Pittier 4373* (NY, US).

2. **Erechtites valerianaefolia** (Wolf) DC., Prodr. 6: 294. 1837.—FIG. 95.

Senecio valerianaefolius Wolf, Ind. Sem. Hort. Berol., teste Reichenb., Icon. Bot. Exot. 59, *tab.* 85. 1827.

Short-lived (monocarpic?) *herb*, 1–2 m tall; glabrous to scattered hispidulous; stems simple or much branched above, striate. *Leaves* alternate, pinnately veined, distinctly petiolate or at most the upper ones merely subsessile, the lower leaf blades ovate to ovate-lanceolate, subentire to variously serrate-dentate, 8–12 cm long, 2–4 cm wide, ca. 3 times longer than wide, well-developed middle leaf blades usually conspicuously pinnatifid-lobulate, the uppermost leaves passing into bracts; petiole in lower and middle leaves about ¼ to ⅓ as long as the blade. *Inflorescence* a variable, paniculate-corymbiform cyme composed of several terminal and upper-axillary cymules. *Heads* turbinate, disciform, ca. 10 mm tall and ca. ⅓ as wide; principal involucral bracts in 1 series, linear subulate, 12–15, sometimes 2 or 3 adjacent bracts weakly connate, especially along the lower ⅓; calyculate bracts thin, linear, sometimes contorted in mature heads; receptacle flat, naked; ray florets in 1–2 series, pistillate, the corolla filiform, tubular; disc florets functional, the innermost apparently more robust and most often fertile. *Achenes* cylindric, striate with ca. 10 ribs, glabrous to minutely pubescent, especially in the grooves; pappus of abundant, soft, capillary hairs, light rose-pink or reddish but sometimes fading to dull white in aging plants, slightly exceeding the involucral bracts in length. Chromosome number $n = 20$.

Erechtites valerianaefolia is a weed in cultivated fields, disturbed sites, and streambanks. It usually occurs above 1,000 m, and has mostly been collected from January to August.

A New World native, now widespread as a weed from Mexico to Argentina, it is also adventive as an aggressive weed in tropical Asia, the Pacific Islands, and northern Australia. Belcher (1956) recognizes 4 formae based foliage variation. Our materials are referable to f. *valerianaefolia*.

BOCAS DEL TORO: N slopes of Cerro Horqueta, *Allen 5010* (MO). CHIRIQUÍ: Vic. of New Switzerland, *Allen 1367* (MO, NY, US). 1 mi E of Cañas Gordas, *Croat 22342* (MO). Side of Cerro Pando, *D'Arcy 5394* (MO). E side of Cerro Pando, *D'Arcy & D'Arcy 6642* (MO). Above Boquete, *D'Arcy & D'Arcy 6475* (MO). Boquete, *Davidson 528* (MO). Valley of upper Río Chiriquí Viejo, vic. of Monte Lirio, *Seibert 164* (MO, NY, US).

FIGURE 95. *Erechtites valerianaefolia* (Wolf) DC.—A–B. Habit (× ½). [After *White 71* (MO).]—C. Head (× 2).—D. Floret (× 2). [After *Liesner 6427* (MO).]

96. LIABUM

Liabum Adanson, Fam. 2: 131. 1763. TYPE: *Amellus umbellatus* L. = *Liabum umbellatum* (L.) Schultz-Bip.

Herbs, subshrubs and *shrubs*; branches soft, densely pubescent or glabrescent, often drying striate-ribbed. *Leaves* opposite, distinct or weakly connate-clasping, green and lightly pubescent to glabrescent above, densely whitish felted-lanate beneath. *Inflorescences* terminal and axillary in the upper leaves, numerous loose to compact paniculate or corymbiform cymes. *Heads* radiate; involucral bracts imbricate in several series; receptacle naked or paleaceous with irregular short awns; ray florets in 1–2 series, fertile, the ligules small, erect or tightly recurved, rolled or long and prominent; disc florets numerous, bisexual, fertile, the style branches linear-subulate to filiform, hirsute, the anthers sagittate. *Achenes* turbinate to weakly 5–(10?) angled, pubescent.

Literature:

Robinson, H. & Brettell, R. D. 1974. Studies in the *Liabeae* (Asteraceae) II. Preliminary survey of the genera. Phytologia 28: 43–63.

a. Plants erect; principal leaves ovate to elliptic or subdeltoid; receptacle naked or loosely paleaceous.
  b. Receptacle paleaceous with short, irregular awns; upper branches whitish felted-lanate; innermost involucral bracts acicular or long-lanceolate ..... 1. *L. bourgeaui*
  bb. Receptacle naked; upper branches brownish, hispid to glabrescent; inner involucral bracts lanceolate-subulate ..... 2. *L. polyanthum*
aa. Plants lax or scrambling; principal leaves triangular; receptacle alveolate .... 3. *L. sagittatum*

1. **Liabum bourgeaui** Hieron. in Ule, Verh. Bot. Vereins Prov. Brandenburg 48: 208. 1907.—FIG. 96.

Coarse *herb* or weakly woody *subshrub*, 1–2 m tall, the upper internodes tightly felted-lanate, dull white to light brown, often streaked with brownish pilose hairs protruding from the lanate tomentum. *Leaves* opposite, pinnately veined with 2 prominent lateral veins arising from near the base, the upper leaf blades ovate to subdeltoid, acuminate above, obtuse to abruptly contracted below to a prominently winged petiole, the margin subentire to minutely denticulate, 10–20 cm long, 7–15 cm wide, ca. 1½ times longer than wide, the upper surface glabrescent to obscurely arachnoid tomentose, the lower surface closely felted-lanate with occasional brownish hairs, usually near the prominent veins; petiole ca. ¼ as long as the blade, the wing acuminate-tapering toward the stem. *Inflorescence* a series of few-headed cymules compounded into an open, terminal, paniculate to corymbiform cyme, usually subtended by prominent and distinct lateral cymes arising in the axils of the upper leaves. *Heads* campanulate, radiate but inconspicuously so; involucral bracts numerous, conspicuously imbricate in several series, acicular to long-lanceolate, glabrous or sometimes arachnoid tomentose among the outermost bracts, the inner and longest bracts often weakly reddish-margined, ca. 8 mm long in mature heads; receptacle paleaceous with irregular subulate awns 2 mm long or less; ray florets in 1–2 series, fertile, the

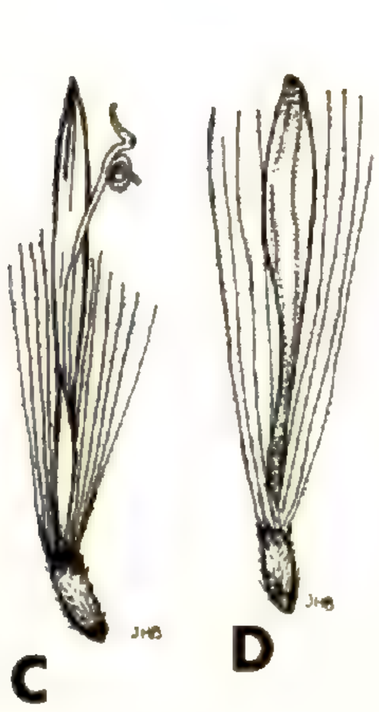

Figure 96. *Liabum bourgeaui* Hieron.—A. Habit (× ½).—B. Head cross section (× 2⅖).—C. Ray floret (× 2⅖).—D. Disc floret (× 2⅖). [After *Liesner 462A* (MO).]

corolla yellowish, ca. 5 mm long, the tube splitting into a narrow ligule about mid-length, the ligule erect and about equalling the style; disc florets numerous, 50–60 (in well developed heads), the corollas thin, early deciduous. *Achenes* turbinate or weakly 5-angled, 1–2 mm long, lightly spreading-pubescent, especially on the angles; pappus straw-colored, uniseriate, capillary, 5–6 mm long.

This species occurs on steep, forested slopes, at elevations of 1,000–2,000 m, but has occasionally been collected at lower elevations. It flowers mostly from January to April.

CHIRIQUÍ: Trail from Paso Ancho to Monte Lirio, 1500–2000 m, *Allen 1587* (MO, NY, US). San Bartolo Limite, 20 km W of Puerto Armuelles, 400–600 m, *Busey* 555 (MO). 2 mi SW of Puerto Armuelles, 0–200 m, *Croat 22042* (MO). Chiquero, 6000 ft, *Davidson 561* (MO, US). El Boquete, 1000–1300 m, *Maxon* 5232 (US). Las Lagunas, 2 mi SW of El Volcán, 4200 ft, *Tyson* 853 (MO). NE of Cerro Pando, 1500 m, *Wilbur et al. 11010* (MO, NY, US). COCLÉ: Cerro Pilón, 700–900 m, *Duke 12068(3)* (MO). El Valle de Antón, 1800 ft, *Paul* (*Maurice 780*) (US). Above Penonomé, *Williams 261* (NY).

2. **Liabum polyanthum** Klatt, Bull. Soc. Roy. Bot. Belgique 31: 209. 1892.

Sinclairia polyantha (Klatt) Rydb., N. Amer. Fl. 34: 299. 1927.

Erect or weakly scandent, terrestrial or epiphytic *subshrub*, 2–3 m tall, arching upward to 8 m or more, the upper internodes short-hispid to glabrescent and usually with scattered, prominent, tuberculate lenticels. *Leaves* opposite, pinnately veined, with 2 prominent lateral veins emerging from near the base; the upper leaf blades elliptic to ovate, the margin denticulate with minute, callose teeth, 7–11 cm long, 3–6 cm wide, to twice as long as wide, the upper surface glabrous or with scattered light arachnoid tomentum, the lower surface with a dense gray-white felted lanate tomentum, the prominent veins short-hispid; petiole prominent, about ¼ to ⅓ as long as the blade. *Inflorescence* an irregular, open paniculate cyme of 40–60 heads in several loose cymules arising terminally and from the axils of the upper leaves. *Heads* campanulate, inconspicuously radiate, at least in dried specimens; involucral bracts imbricate in 3–4 series, the innermost 4–6 mm long, lanceolate-subulate, often reflexed-spreading at maturity, brownish pubescent outside, especially toward the margin, or occasionally glabrate, the margin sometimes prominently long-villous; receptacle naked; ray florets yellow or ochroleucus to creamy-white, fertile and inconspicuous, few (5–8?), the corolla short and recurved-rolled in dried specimens; disc florets yellow to creamy-white, ca. 20, the corollas exceeding the involucre by 1–2 mm. *Achenes* turbinate to weakly angled, ca. 1 mm long, appressed-pubescent; pappus of both disc and ray florets persistent and conspicuously protruding beyond the involucre, composed of numerous yellow-white, brittle, barbellate bristles, 8–10 mm long, interspersed by several scarious, narrowly subulate awnlike bristles ca. 0.5 mm long.

Liabum polyanthum occurs in openings or disturbed places in wooded areas, usually above 1,000 m. It flowers from December to January.

CHIRIQUÍ: Vic. of New Switzerland, 1800–2000 m, *Allen 1415* (MO, NY, US). Alto Lino, 4200 ft, *Maurice 836* (MO, US). Chiriquí Viejo Valley, *White* 93 (MO, US). COCLÉ: Hills N of El Valle de Antón, 1000 m, *Allen 2347* (US). Region of El Valle de Antón, 1000 m, *Allen 2886* (MO, US). Slopes of Cerro Pilón near El Valle, 700–900 m, *Duke 12068* (NY). Cerro Pilón, 3000 ft, *Duke & Lallathin 14994* (MO, NY), *15011* (MO). El Valle, *Gentry & Dwyer 3673* (MO). COLÓN: Santa Rita Ridge, *Dwyer & Gentry 9370* (MO). PANAMÁ: Goofy Lake, *Dwyer 7052* (MO, US). Cerro Jefe to La Eneida, 3100 ft, *Dwyer et al.* 8229 (MO). Cerro Jefe, 3100 ft, *Dwyer & Gentry* 9438 (MO, NY). Cerro Campana, *Ebinger* 235 (MO). *Lewis et al. 3062* (MO).

3. **Liabum sagittatum** Schultz-Bip., Flora 36: 37. 1853.

Munnozia sagittata (Schultz-Bip.) H. Robinson & Brettell, Phytologia 28: 56. 1974.

Lax, scrambling or trailing *liana*, the upper internodes densely but irregularly arachnoid-villous, glabrescent. *Leaves* opposite, petiolate; blades triangular, sharply truncate to weakly hastate at the base, shallowly serrate-dentate, 5–9 cm long, 2.5–4 cm wide, twice as long as wide, the upper surface green, glabrous, occasionally with scattered hairs, or sometimes pubescent along the prominent large veins, the lower surface densely gray-white lanate; petiole ca. ½ as long as the blade, basally expanded and connate-perfoliate in pairs. *Inflorescence* an open, compound cluster of long-pedunculate dichasia, arising terminally and in the axils of the uppermost leaves. *Heads* yellow, large and conspicuous, the disc 1–2 cm across (exclusive of rays) when dried; involucral bracts thin, imbricate in ca. 3 series, the largest 5–10(–15) mm long, 2–4(–5) mm wide, broadly oblanceolate, the margins scarious-fimbriate to coarsely pubescent; receptacle flat to weakly convex; paleas of irregular lengths, thin, lacerate, marginally fused and forming alveolae surrounding the individual achenes; ray florets 20–40 in 1–2 series, the tube short-pubescent on the lower ⅓, the ligule conspicuous, 15–20 mm long in dried specimens; disc florets numerous, the corolla deeply parted into 5 prominent lobes, the style branches without conspicuous appendages. *Achenes* 1–1.5 mm long, reddish-brown except for a white torus-apophysis at the base, weakly fusiform with ca. 10 prominent ribs and a few conspicuous long hairs on the ribs, glabrate at maturity; pappus a single series of yellow-white capillary bristles 5–7 mm long.

Liabum sagittatum is known in Panama only from elevations of 2,300 m and above in the region of Cerro Punta, Chiriquí Province. Flowering collections have been made from December through May.

CHIRIQUÍ: Trail from Cerro Punta to headwaters of Río Caldera, 2250–2500 m, *Allen 1458* (US). Cerro Punta, 7000 ft, *Blaisdell 342* (US). Trail N of Cerro Punta, *Croat 10436* (MO). Slopes of Las Cumbres near Cerro Punta, *Croat 13671* (MO). Ca. 2 mi E of Cerro Punta, 6900 ft, *Wilbur et al. 13128* (MO). Trail from Bajo Grande along the Quebrado Grande, 2100–2400 m, *Wilbur et al. 15162* (MO). Guadalupe, *Wilbur et al. 15329* (MO).

97. NEUROLAENA

Neurolaena R. Br., Trans. Linn. Soc. London 12: 120. 1817. TYPE: *Conyza lobata* L.= *Neurolaena lobata* (L.) R. Br.

Coarse *herbs* with soft, pithy stems, variously covered by an appressed to spreading rough tomentum. *Leaves* alternate, the upper ones subentire to dentate, the lower ones sometimes deeply lobed. *Inflorescence* a many-headed, terminal and upper-axillary, compound, corymbiform cyme. *Heads* discoid; involucral bracts imbricate in 3–4 series; receptacle flat; paleas copious, membranous; florets numerous, the style branches thin, abruptly terminated in a crest of short hairs, the anther bases minutely sagittate. *Achenes* terete or weakly 5-ribbed, lightly pubescent, especially on the angles; pappus abundant in 1–2 series.

The relationships of this genus have been discussed by Robinson & Brettell (1973).

1. **Neurolaena lobata** (L.) R. Br., Trans. Linn. Soc. London 12: 120. 1817.—FIG. 97.

Conyza lobata L., Sp. Pl. 862. 1753.

Coarse *herb* or *subshrub* 1.5–3 m tall; stems soft, terete, with abundant pith, covered with an appressed to lightly spreading strigose tomentum. *Leaves* alternate, oblanceolate to narrowly elliptic, tapering to a short petiole, pinnately veined, the margin commonly serrate-denticulate to entire, sometimes deeply lobed, especially the lower leaves, the middle and upper leaves 2–4 cm wide, 8–20 cm long, and about 4–5 times longer than wide, the well-developed lower leaves sometimes much larger and relatively broader, the upper surface lightly glandular-scabrous with short, stiff appressed hairs, the lower surface with a weakly spreading strigose tomentum. *Inflorescence* a series of loose to dense clusters of bracteate corymbiform cymes, the pedunculate cymes terminal or lateral from the axils of the upper leaves. *Heads* discoid, campanulate, small, (3–)4–6(–8) mm tall when dried but varying greatly with degree of maturity and perhaps from plant to plant; involucral bracts imbricate in 3–4 series, oblong, stramineous-chartaceous, especially distally; receptacle with numerous thin paleas about as long as the inner involucral bracts; florets yellow or occasionally yellow-green or white, ca. 30 (in well-developed heads), about as long as the involucral bracts. *Achenes* black or gray-brown, ca. 2–4 mm long, terete or obscurely 5-ribbed, lightly pubescent on the angles; carpopodium small but prominent, dull yellow-white; pappus of copious, whitish, lightly barbellate bristles slightly exceeding the involucral bracts at maturity.

This species is widespread in wooded areas, clearings and disturbed sites, usually below 800 m elevation. It flowers virtually the year round but has been most frequently collected from December to March.

BOCAS DEL TORO: Water Valley, Chiriquí Lagoon, *von Wedel 1790, 1821* (both MO, US). Old Bank Island, Chiriquí Lagoon, *von Wedel 1866* (MO, US), *1914, 1966* (both MO). CANAL ZONE: Galen Point, *Blum & Dwyer 2142* (MO). Barro Colorado Island, *Croat 5292, 7223, 7224, 8302, 8381, 9112* (all MO). N of Paraíso, *Croat 12975* (MO). Chagres, *Fendler 155* (MO, US). Between Summit and Gamboa, *Greenman & Greenman 5230* (MO). Gatún, *Hayes 624* (NY). Between Gamboa and Darién, *Heriberto 23* (US). Barro Colorado Island, *Hladick 105* (MO). Chagres River, 3 mi above Gamboa, *Kennedy et al. 2296* (MO). Chiva-Chiva Trail, *Piper 5768* (US). Barro Colorado Island, *Silvestre 607* (MO). Balboa, *Standley 27003* (US). Las Cascadas Plantation near Summit, *Standley 29502* (US). Frijoles, *Standley 27620* (US). Fort Sherman, *Standley 30977* (US). Barro Colorado Island, *Standley 41070* (US). 1 mi N Summit, *Tyson et al. 2780* (MO). 6 mi N Gamboa, *Tyson 3490* (MO). Fort San Lorenzo, *Tyson & Blum 3687* (MO). CHIRIQUÍ: Boquete, *Allen 4652* (MO). 9 km from Puerto Armuelles, *Busey 741* (MO). 2 km N of Punta de Burica, *Busey 748* (MO). Vic. of Boquete, *Lewis et al. 587* (MO). Around El Boquete, *Pittier 2977* (US). COCLÉ: El Valle, *Allen 1198* (MO). N of El Valle de Antón, *Allen 3714* (MO). Hills above El Valle de Antón, *D'Arcy & D'Arcy 6767* (MO). El Valle de Antón, along Río Indio trail, *Hunter & Allen 305* (MO). Boca del Toabre, *Lewis et al. 5510* (MO, NY). COLÓN: Río Viejo, vic. of Puerto Pilón, *Allen 4101* (MO). Miguel de la Borda, *Croat 10031* (MO). Between Salud and Boca de Río Indio, *Howell 68* (MO). Santa Rita Ridge, *Lewis et al. 5375* (MO). Between France Field and Cativa1, *Standley 30198* (US). DARIÉN: Between Pinogana and Yavisa, *Allen 239* (MO, NY). Río Pirre, 2–5 mi above El Real, *Duke 5085* (MO, US). Río Pirre, ca. 10 mi S of El Real, *Duke 5460* (MO). Cerro Pidiaque, *Duke 8081(2)* (MO). Manené, *Kirkbride & Bristan 1609*

Figure 97. *Neurolaena lobata* (L.) R. Br.—A. Habit (× ½).—B. Head (× 5). [After *Dwyer 2130* (MO).]—C. Leaf (× ½). [After *Narvaez 3185*, Nicaragua (MO).]

(MO). Camp Summit, Darién—San Blas border, *Oliver et al. 3680* (MO). Along the Sambú River, *Pittier 5539* (US). Between Paya and Boca de Paya, *Stern et al. 271* (MO, NY, US). Vic. of Campamento Buena Vista, *Stern et al. 875* (MO, US). Chipijana District, *Terry & Terry 1387* (MO). Cerro Piriaque, *Tyson et al. 3827* (MO). LOS SANTOS: Loma Pieta, *Duke 11841(2)* (MO). 17.8 mi S of Macaracas, *Lewis et al. 1603* (MO, US). S of Macaracas at Quebrada Bejuco, *Tyson et al. 2913, 2930, 3061* (all MO). PANAMÁ: Cerro Azul, *Croat 17321* (MO); *Duke 9365* (MO). Tocumen, *Dwyer 2891* (MO). San José Island, *Erlanson 49, 220* (both US). Cerro Campana, *Luteyn & Kennedy 1797* (US). Near Tapia River, *Killip 3323* (US). Cerro Jefe, *Kirkbride & Crebbs 3* (MO, NY). 2–3 mi S of Goofy Lake, *Lewis et al. 237* (MO, NY, US). 5 mi SW of Cerro Brewster, *Lewis et al. 3385* (MO). Road from El Llano

to Cartí-Tupile, *Leisner 705* (MO). Near Tapia River, *Maxon & Harvey 6669* (US). Hills around Allajuela, *Pittier 2337* (US). Río Tapia, *Standley 28058* (US). Cerro Jefe, *Tyson et al. 3186, 4303, Tyson 3363* (all MO). Road from Cerro Azul to Cerro Jefe, *Tyson 6314* (MO).

98. SCHISTOCARPHA

Schistocarpha Less., Linnaea 6: 409. 1831. TYPE: *S. bicolor* Less.

Large coarse *herbs* or *subshrubs*. *Leaves* opposite, distinctly or weakly connate-clasping at the nodes, the uppermost leaf blades basally attenuate into a weakly-winged petiole. *Inflorescence* a conglomerate corymbiform to paniculate cyme composed of many terminal and upper-axillary cymules. *Heads* radiate or disciform; involucral bracts imbricate in 3–4 series; receptacle convex to hemispherical or even conical; paleas abundant, unequal; ray florets fertile, small, numerous, in 1–2 series, the ligule short, thin and inconspicuous, or sometimes well developed; disc florets numerous, fertile, the anther bases weakly sagittate, the style branches slender, abruptly terminated in a small, tufted crest of hairs. *Achenes* terete or weakly ribbed, glabrous.

a. Ray florets inconspicuous in 1–2 series; ligules erect or weakly reflexed-spreading, 1 mm long or less; widespread species ..... 2. *S. oppositifolia*
aa. Ray florets prominent in ca. 3 series; ligules regularly spreading at right angles to the tube, 2–5 mm long; Chiriquí species ..... 1. *S. croatii*

1. **Schistocarpha croatii** H. Robinson, Phytologia 29: 339. 1975. TYPE: Panama, *Croat 26411* (MO, holotype).—FIG. 98A–B.

Erect, sparsely branched *subshrub*, 1–2 m tall, lightly short-pilose. *Leaves* opposite, ovate, acuminate above, cuneate at the base, serrate; blades 6–10 cm long, 2.5–5.0 cm wide, 2–3 times longer than wide, narrowly decurrent at the base, the midvein densely pilose beneath; petiole 1.5–4.0 cm long. *Inflorescence* a series of loose, open paniculate cymes. *Heads* narrowly campanulate, 7–8 mm tall, 7–8 mm wide; involucral bracts imbricate in ca. 4 series, oblong to broadly oblong, round-obtuse apically, the margins puberulous; receptacle paleaceous; paleas subscarious, laciniate; ray florets 40–60 in 2–3-series, the tube slender and densely pubescent, expanding into a prominent, white, lobed ligule 2–5 mm long and 0.5 mm wide; disc florets 30–40, white, the corolla 4–5 mm long, hispidulous. *Achene* glabrous, ca. 1 mm long, distinctly ribbed; pappus of prominent, early deciduous, capillary bristles.

This species is found in forest openings at elevations of 2,000 m and above in the mountains of Chiriquí. It flowers mostly in February, but has also been collected in July.

CHIRIQUÍ: W slopes of Cerro Horqueta, *Allen 4813* (MO). Slopes of Las Cumbres near Cerro Punta, *Croat 13770* (MO). Bajo Chorro, Boquete, *Davidson 337* (MO, US).

2. **Schistocarpha oppositifolia** (Kuntze) Rydb., N. Amer. Fl. 34: 306. 1927.—FIG. 98C.

Zycona oppositifolia Kuntze, Rev. Gen. Pl. 373. 1891.
Schistocarpha hoffmannii Kuntze, Rev. Gen. Pl. 3: 170. 1898.

Erect, branching, coarse *herb* or *subshrub*, 1–3 m tall; stems terete, striate, sparsely short villous-pilose along the internodes, usually more densely pubescent

FIGURE 98. *Schistocarpha*.—A–B. *S. croatii* H. Robinson.—A. Habit (× ½).—B. Ray floret (× 6⁹⁄₁₀). [After *Croat 26411* (MO).]—C. *S. oppositifolia* (Kuntze) Rydb. Ray floret (× 9⅕). [After *Croat 23902* (MO).]

at and near the nodes. *Leaves* opposite, pinnately veined, the well-developed upper leaves ovate, basally truncate to obtuse, the uppermost leaves becoming lanceolate and weakly attenuate at the base, the margins serrate to dentate, often with minute, callose teeth (6–)10–15 cm long, 3–7 mm wide, ca. 2 times longer than wide, the upper surface scattered viscid-glandular pilose to glabrate, the lower surface with a loose scattered tomentum, sometimes densely pilose on the

veins; petiole distinct, ca. ⅓–½ as long as the blade. *Inflorescence* of corymbiform cymules, each cymule with 6–10 heads, arising terminally or laterally from the axils of the uppermost leaves. *Heads* campanulate, inconspicuously radiate, yellow to yellow-green or sometimes white; involucre ca. 1 cm tall, 1 cm across when dried, the bracts imbricate in 3–4 series, the innermost 6–7 mm long, stramineous-chartaceous at maturity, often long-pubescent on the margins; receptacle convex; paleas thin, unequal; ray florets in 1–2 series, scarcely exceeding the involucre, the tube narrow-filiform with a short, erect ligule less than 1 mm long; disc florets ca. 60–70 in well-developed heads, slightly exceeding the involucre in length. *Achene* narrowly fusiform, terete or weakly 5-ribbed, ca. 1 mm long, black; pappus a uniseriate series of white, minutely barbellate capillary hairs.

This is a species of forests, especially openings and disturbed areas. It has been found mostly below 1,000 m in elevation, occasionally higher, in the mountains of Chiriquí. It flowers the year round but has frequently been collected in July and August.

BOCAS DEL TORO: Forest above RR stop at mi 7.5, *Croat & Porter 16226* (MO). Water Valley, *von Wedel 930* (MO). Nievecita, *Woodson et al. 1822* (MO). CANAL ZONE: Madden Forest, *Croat 12248* (MO). Vic. of Fort San Lorenzo, *Croat 12519* (MO). Madden Forest, *D'Arcy & D'Arcy 6096* (MO). Between Madden Dam and Saddle 11 near Alajuela, *Dodge et al. 16501* (MO). Ca. 1 mi S of Madden Dam, *King 5237* (US). Margarita swamp, S of France Field, *Maxon & Valentine 7056* (US). Howard Air Force Base, *Tyson 1863* (MO, US). Fort San Lorenzo, *Tyson 3505* (MO). Gamboa, *Tyson et al. 4568* (MO). CHIRIQUÍ: Above Cerro Punta on road to Cerro Respinga, *D'Arcy & D'Arcy 6512* (MO). Valley of the upper Río Gariché, *Siebert 356* (MO). COCLÉ: Between Cerro Pilón and El Valle de Antón, *Duke & Dwyer 13927* (MO). El Valle, *Dwyer 1907* (MO). COLÓN: Portobelo, *D'Arcy 4071* (MO). Santa Rita Ridge, *D'Arcy & D'Arcy 6161* (MO). Portobelo, *D'Arcy 6692* (MO); *Dwyer 4396* (MO). Quebrada Maskia off Río Pucro above Pucro, *Duke 13094(3)* (MO). LOS SANTOS: From 1 mi S to 10 mi S of Tonosí, *Duke 12495(1)* (MO). Los Toretos, *Dwyer 2454* (MO, US). Headwaters of Río Pedregal, *Lewis et al. 2916* (MO). PANAMÁ: 10 km N of El Llano, *Busey 916* (MO). 3 mi above Goofy Lake, *Croat 11582* (MO). S of Cañita, *Croat 14511* (MO). 7 mi from highway on road to Cerro Jefe, *Croat 15182* (MO). Cerro Azul, *Dwyer 2648* (MO). Between Cañita and dam site, *Gentry & Tyson 1708* (MO). 0–2.5 mi along lumber road to Río Maestro, *Gentry 2354* (MO). Near Bayano Dam E of Cañitas, *Gentry 5567* (MO). S slopes of Cerro Azul, *King 5254* (US). Junction of Ríos Pacora and Corso, *Oliver 2365* (MO). Cerro Azul, *Porter et al. 4084* (MO). Arraiján, *Woodson et al. 1394* (MO, NY). Nievecita, *Woodson et al. 1822* (NY, US).

99. SENECIO

Senecio L., Sp. Pl. 866. 1753; Gen. Pl., ed. 5. 375. 1754. TYPE: *S. vulgaris* L.

Herbs, shrubs, small *trees* or *lianas. Leaves* alternate, simple, pinnately veined, or in 1 species, palmately veined. *Inflorescence* a few–many-headed corymbiform cyme arising terminally or in the axils of the upper leaves, or occasionally heads solitary. *Heads* radiate or discoid, rarely disciform, red to orange-red or yellow, sometimes ochroleucous; principal involucral bracts of equal length in a single series or obscurely divisible into an inner and outer series, usually subtended by a calyculus of 10 or fewer irregular bractlets; receptacle flat to gently convex, naked, sometimes obscurely alveolate or with minute hairlike paleas irregularly disposed among the achenes, conspicuous paleas lacking; ray florets fertile, in a single series, the ligule usually well developed but sometimes reduced and inconspicuous,

ray florets sometimes absent; disc florets fertile, bisexual, the style branches variously tipped with a penicilliate tuft of hairs to a distinct, triangular appendage. *Achene* terete or ribbed, glabrous or variously pubescent; pappus of a single series of white, capillary bristles.

A huge complex of more than 1500 species in both the Old and New Worlds, *Senecio* is readily divisible into semidistinct groups. Some contemporary botanists advocate the recognition of several segregate genera, but the broad traditional concept of *Senecio* has been maintained in this treatment.

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Williams, L. O. 1975. Tropical American plants, XVIII. Phytologia 31: 435–447.

a. Erect herbs, shrubs or small trees, not scrambling lianas.
  b. Cauline leaves palmately veined ..... 6. *S. heterogamus*
  bb. Cauline leaves pinnately veined.
    c. Leaves densely white lanate-tomentose throughout, at most glabrate on the upper leaf-surfaces ..... 8. *S. oerstedianus*
    cc. Leaves variously pubescent to glabrous but not densely white-lanate-tomentose.
      d. Leaves large, blades 15–35 cm long, deeply sinuate with 3–6 conspicuous sinuses on each side of the leaf ..... 2. *S. arborescens*
      dd. Leaves normally smaller, dentate to entire but not both large and deeply sinuate.
        e. Involucral bracts 13–17(–18), the calyculate (basal) bracts 6 or more, conspicuous, often more than 5 mm long, the involucre often purplish ..... 3. *S. boquetensis*
        ee. Involucral bracts ca. 8, the calyculate (basal) bracts 4 or fewer, rarely more than 4 mm long.
          f. Heads narrowly cylindrical; involucral bracts linear-oblong, more than 8 mm long; ligules ca. 10 mm long in dried specimens ..... 5. *S. cooperi*
          ff. Heads broader upwards, at least at maturity; involucral bracts lanceolate-spatulate, 6–7 mm long; ligules 5–8 mm long .. 7. *S. megaphyllus*

aa. Lianas.
  g. Heads large, campanulate; principal involucral bracts 30–40; ray florets 18–24, the style branches surmounted by distinctly expanded, papillose, triangular tips ..... 4. *S. confusus*
  gg. Heads smaller; principal involucral bracts 10 or fewer; style branches surmounted by penicilliate hairs.
    h. Heads radiate, the ligules long and narrow, ca. 10–15 mm long, less than 1 mm wide; leaves, especially the lower surfaces, with stipitate-stellate hairs ..... 1. *S. angustiradiatus*
    hh. Heads disciform or with ligules less than 1 mm long; leaves glabrescent, sometimes with scattered simple hairs ..... 9. *S. parasiticus*

1. **Senecio angustiradiatus** Barkley.[62] TYPE: Panama, *Dressler 4616* (MO).

Liana, variously covered with light reddish-brown pubescence of stipitate-stellate hairs with stalks 0.5–0.8 mm long arising from swollen bases and with 5–6 straight or curved radiating arms, especially on hairs along the upper stems, among the heads in the inflorescence and on the undersides of the leaves, simple hairs of the same color occurring among the stipitate-stellate hairs, especially on the outside of the involucral bracts, near the base of the heads, and on the upper peduncles. *Leaves* evenly distributed along the stem, alternate, entire, broadly elliptic to ovate, inconspicuously acuminate, rounded at the base, sometimes weakly revolute at the margins, pinnately veined, 7–10 cm long, 3.5–5 cm wide, twice as long as wide, coriaceous or at least appearing so in dried specimens, glabrescent, the upper surface with a few scattered hairs, the lower surface pubescent with stipitate-stellate hairs; petiole distinct, ca. 1 cm long, attached to the stem just above a pubescent, pulvinate bud-scale scar. *Inflorescence* a series of racemose or paniculate cymes, each with 10–20 heads, arising in the axils of the upper leaves. *Heads* campanulate at maturity, conspicuous with red-purplish involucral bracts, yellow corollas and narrow rays; involucral bracts 8–10, lanceolate, slightly acuminate, 7–10 mm long, 2–3 mm wide; calyculate bracts 1–3, lanceolate, 3–4 mm long; receptacle slightly convex with scattered, hyaline, bristlelike paleas 0.5–1 mm long, irregularly interspersed between the achenes; ray florets 5, the tube 5–6 mm long, the ligule distinct, narrow-filiform, 10–12 mm long, 0.5–1 mm wide, usually tortuous-recurved in dried specimens; disc florets 10–15, the tube 5–6 mm long, the limb 4–5 mm long, the style branches tipped with a small tuft of translucent hairs. *Achene* reddish-brown, columnar, terete or weakly angled, glabrous, 1–2 mm long; the pappus a single series of white, capillary bristles protruding 3–5 mm beyond the involucre.

This entity is known to me by only two specimens, but the narrow rays, the reddish-purple involucres, and the peculiar stipitate-stellate pubescence combine to make it distinct. Both collections were taken in flower in March.

COCLÉ: Cerro Pilón, 900–1173 m, *Liesner 789* (MO). PANAMÁ: El Llano-Cartí highway, ca. 10–12 km N of El Llano, *Dressler 4616* (MO).

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[62] *Senecio angustiradiatus* Barkley, sp. nov. *Frutex* scandens modo variabili sed praecipue secus ramulos summos, inter inflorescentiae capitula foliorumque dorso pilis rufis 0.5–0.8 mm longis basi dilatatis apice stellatim 5–6-radiatis, ulterius praecipue ad involucri bracteas, capitulorum basin summosque pedunculos pilis simplicibus concoloribus immixtis conspersa, foliis adultis glabrescentibus. *Folia* regulatim secus ramulos ordinata alterna, late elliptica vel ovata subacuminata, basi rotundata, margine integra nunc subrevoluta, 7–10 × 3.5–5 cm, bis longiora quam lata, pennivenia; petiolo ± 1 cm longo proxime supra perulae cicatricem pulvinatum orto; lamina (sicca) coriacea. *Inflorescentiae* e cymis axillaribus subterminalibusque racemosis vel paniculatis 10–20-capitulatis compositae. *Capitula* matura campanulata, bracteis involucralibus 8–10 lanceolatis subacuminatis 7–10 × 2–3 mm rubro-purpureis, calyculi bracteolis 1–3 lanceolatis 3–4 mm longis; receptaculo subconvexo paleis hyalinis setiformibus 0.5–1 mm longis inter achaenia hinc inde consperso; radii flosculorum 5 tubo 5–6 mm longo, ligula anguste filiformi 10–12 × 0.5–1 mm, sicca saepissime contortuplicatim recurva; disci flosculorum 10–15 tubo 5–6 mm, limbo 4–5 mm longis; styli ramulis apice pilis hyalinis penicillatis; pappi 1-seriati setis capillaribus albis, involucrum 3.5 mm superantibus; achaenio columnari 1–2 (+?) mm longo tereti vel subangulato rufo glabro.

2. **Senecio arborescens** Steetz in Seem., Bot. Voy. Herald 162, *tab. 31.* 1854. TYPE: Panama, *Seemann 1163* (BM, not seen).

Telanthophora arborescens (Steetz) H. Robinson & Brettell, Phytologia 27: 426. 1973.

Shrub or small *tree*, to 9 m tall; closely lanate-pubescent and scattered-tufted villous, especially among the branches of the inflorescence and along the veins on the leaf undersides, irregularly glabrescent. *Leaves* alternate; blades 15–35 cm long, 10–20 cm wide, ca. 1½ times longer than wide, broadly ovate to obovate, regularly sinuate with 3–6 sinuses on each side of the midvein, the sinuses extending about halfway to the midvein, the lobes subentire or callose-denticulate, the venation pinnate; petiole distinct, ⅓ as long as the blade. *Inflorescence* a loose to open compound of corymbiform cymules, forming an arching inflorescence 20–30 cm across with 200–400 heads. *Heads* yellow, at least sometimes fragrant; principal involucral bracts 5–6 mm long, ca. 8 in number, arranged in 2 alternating series, the outer bracts linear-lanceolate, ca. 1 mm wide, the margins scarious but not hyaline, the inner bracts oblanceolate-oblong, ca. 2 mm wide, the margins distinctly scarious-hyaline; calyculate bracts 1–3, linear, 2–3 mm long; receptacle flat with irregular, minutely denticulate paleas; ray florets 3(–5), the tube 3–4 mm long, the ligule ca. 4 mm long, less than 1 mm wide in dried specimens; disc florets 8–10, the corolla 6–7 mm long, not sharply separated into tube and limb. *Achene* columnar, terete or weakly angled, glabrous, 3–4 mm long; pappus of white, uniseriate, capillary bristles, exceeding the involucre by 1–3 mm or more.

This species is a small, understory tree or shrub in clearings and along streambanks, occurring at 1,500–2,300 m elevation in the mountains of Chiriquí Province. It flowers from February to June, but is most often collected in March.

The name *Senecio copeyensis* Greenman has been used for some Panamanian material properly referred to *S. arborescens*. The epithet *copeyensis* applies to an eradiate entity of Costa Rica.

CHIRIQUÍ: Trail from Bambito to Cerro Punta, *Allen 307* (MO). Nueva Swissa, *Croat 13502* (MO, NY). Bajo Mono, Boquete, *Davidson 465* (US). Cerro Punta, *Kozlovsky K-7* (MO). Río Ladrillo, above El Boquete, *Stern et al. 1972* (MO, US). Finca Collins, vic. of El Boquete, *White 7* (MO, US). Upper Río Chiriquí Viejo, *White 330* (MO). Volcán de Chiriquí, *Woodson et al. 905* (MO).

3. **Senecio boquetensis** Standley, Publ. Field Mus. Nat. Hist., Bot. Ser. 22: 394. 1940. TYPE: Panama, *Pittier 5382* (F, holotype, not seen; US, isotype).

Erect *herb* or *subshrub*, 1–2 m tall, the upper and middle nodes often swollen, the middle internodes variously lanate-villous to arachnoid, glabrescent. Middle cauline *leaves* alternate, 6–12 cm long, 3–7 cm wide, about twice as long as wide, lanceolate to narrowly elliptic, tapering basally to a conspicuously lobulate-undulate, winged petiole, sometimes with 2–3 pairs of prominent lateral lobes, pinnately veined, the margins serrate-dentate, callose-denticulate, closely short-pilose above, densely to irregularly lanate-villous beneath; petiole about as long as the blade or slightly less, basally clasping; upper cauline leaves reduced to sessile, clasping, deeply serrate to parted bracts, 3–7 cm long. *Inflorescence* a loose to tight agglomeration of 1–6 corymbiform cymules of 8–15 heads each, arising

terminally or from the axils of upper cauline leaves; peduncles sparsely pilose to glabrate, sometimes purplish. *Heads* with orange florets and purple or near-purple involucres, sometimes parasitized by an insect gall in the receptacle; principal involucral bracts 13–17(–18), elliptic-lanceolate, tapering to a weakly erose apex, (7–)8–9 mm long; calyculate bracts 6–10, conspicuous, spreading or sometimes reflexed, linear-subulate, 5–10 mm long; receptacle flat, subalveolate with short irregular teeth (paleas) projecting ca. 0.5 mm upwards between the achenes; ray florets ca. 8 but sometimes absent, even on some plants with otherwise radiate heads, the tube 5–6 mm long, the ligule 9–12 mm long, 2–3 mm wide in dried specimens, sometimes irregularly 2–3-lobed apically; disc florets 20–30, the corolla 6–9 mm long at anthesis, not sharply distinguished into tube and limb, the lobes conspicuous with sinuses 2–3 mm deep. *Achene* columnar or weakly fusiform, 2–3 mm long, hispid-hirsute, sometimes sparingly so; pappus a single series of white capillary bristles, equalling or slightly exceeding the involucre.

Senecio boquetensis occurs in open, damp rocky sites or disturbed swampy places at 1,000–3,000 m elevation in the mountains of Chiriquí Province. Flowering specimens were collected from December to January but one specimen was collected in April.

CHIRIQUÍ: Upper valley of Río Chiriquí Viejo, *Allen 1586* (MO). N of Volcán City, *Duke 9029* (MO). Vic. of Boquete, *Lewis et al. 353* (MO). Between Cerro Vaca and Hato de Loro, *Pittier 5382* (US). Chiriquí Viejo Valley, *White 94* (MO). Between El Hato and Volcán de Chiriquí, *Wilbur et al. 15397* (MO).

4. **Senecio confusus** Britten, Jour. Bot. 36: 260. 1898, based on *Gynoxys berlandieri* DC., not *Senecio berlandieri* Schultz-Bip. (1845).

Gynoxys berlandieri DC., Prodr. 6: 326. 1837. TYPE: Mexico, *Berlandier* (not seen).
G. cumingii Benth. in Örst., Vidensk. Meddel. Dansk Naturhist. Foren. Kjøbenhavn 1852: 109. 1852. TYPE: Costa Rica, *Örsted* (not seen).
Senecio benthamii Griseb., Abh. Königl. Ges. Wiss. Göttingen 24: 206. 1879, not *Senecio benthamii* Wedd. (1859). SYNTYPES: Nicaragua, *Wright*. Panama, *Seemann*. Paraguay, *Balansa* (none seen).
S. *berlandieri* (DC.) Hemsley, Biol. Centr. Amer., Bot. 2: 236. 1881, not S. *berlandieri* Schultz-Bip. (1845).
S. *calocephalus* Hemsley, Biol. Centr. Amer., Bot. 2: 237. 1881, based on *Gynoxys cumingii* Benth., not *Senecio calocephalus* Poepp. & Endl. (1845).
S. *hemsleyi* Britten, Jour. Bot. 36: 260. 1898, new name for *Gynoxys cumingii* Benth., not *Senecio cumingii* Hook. & Arn. (1841).
Pseudogynoxys berlandieri (DC.) Cabr., Brittonia 7: 56. 1950.

Herbaceous *liana*, climbing over other vegetation and on natural and man-made escarpments; stems conspicuously striate, at least in dried specimens, glabrate or villous to loose-pilose, especially in and near the axils of peduncles, glabrescent. *Leaves* alternate; blades 6–12 cm long, 2–7 cm wide, ca. 2–3 times longer than wide, lanceolate to ovate-lanceolate, rounded to contracted or sometimes cordate at the base, the margin shallow-serrate or dentate to subentire, the teeth callose-denticulate, the venation pinnate; petiole distinct, 1–2 cm long but uppermost leaves becoming sessile. *Inflorescence* of 1–2(–3) large heads supported by a conspicuous peduncle 10–30 cm long, arising from axils of the

uppermost leaves, sometimes with 1–5 reduced, bractlike leaves arising along the peduncle. *Heads* campanulate at maturity, red or orange-red to bright orange, large; disc 2–2.5(–3) cm across; principal involucral bracts 30–40, narrowly lanceolate to acicular, gradually acuminate, sometimes red-pink tipped, lightly puberulent or pilose on the outer midrib, 8–12 mm long; calyculate bracts prominent and numerous, irregularly spaced and at most ca. ½ as long as the principal involucral bracts, pubescent-pilose on the outside and often along the margins; receptacle gently convex, distinctly shallow-alveolate; ray florets 18–24 in a single whorl, the tube ca. 7 mm long, the ligule 10–15 mm long, 3–4 mm wide in dried specimens; disc florets numerous, 40–60, the corolla 10–12 mm long, the tube and limb not sharply distinguished, the lobes prominent, the sinuses ca. 2 mm deep, the style branches with expanded, papillose, triangular tips. *Achene* columnar, with ca. 10 prominent ribs, lightly pubescent, 4 mm long, 0.8 mm wide; pappus of white, uniseriate, capillary bristles.

This species ranges from sea level to ca. 800 m elevation, probably throughout Panama, in areas of disturbance. Apparently native, it has been distributed by man as an ornamental.

This species and its neotropical relatives were called section *Convolvuloidei* by Greenman (1901), and have been segregated as the genus *Pseudogynoxys* (Cabrera, 1950). They are characterized by distinctive, triangular style apices and a climbing habit. The group has its share of nomenclatural confusion, and a complete synonymy for *Senecio confusus* must await a thorough revision of the group. Williams (1975) resurrected the name *S. chenopodioides* H.B.K. (1820) for this complex but did not fully document the nomenclature or the taxonomy. He did not cite types or indicate that types were studied.

BOCAS DEL TORO: Changuinola Valley, *Dunlop 541* (US). CANAL ZONE: Road to Lapita signal station near Summit, *Croat 13956* (MO). Culebra Cut, *Hunter & Allen 780* (MO, US). Empire to Mandinga, *Piper 5473* (US). Around El Paraíso, *Pittier 2530* (MO, US). Las Cascadas Plantation, near Summit, *Standley 29577* (US). COCLÉ: Road to El Cope from Interam. Hwy., *Burch et al. 1369* (MO, US). Village of El Valle, *Dwyer 11941* (MO). Mountains beyond La Pintada, *Hunter & Allen 548* (MO). Bismark, above Penonomé, *Williams 314* (MO), *Williams 599* (MO, NY, US). HERRERA: Banks of Río Santa María, *Burch et al. 1202* (MO). Road from La Avena to outskirts of Pesé, *Burch et al. 1313* (MO, US). Near river at Ocú, *Croat 9648* (MO). Between Ocú and Chitré, *D'Arcy 4147* (MO). 4 mi S of Los Pozos, *Tyson 2638* (MO). LOS SANTOS: Ca. 5 mi S of Las Tablas, *Burch et al. 1246* (MO, US). 5 mi E of Macaracas, *Tyson et al. 3133* (MO). PANAMÁ: Vic. of Arraiján, *Allen 1624* (US). VERAGUAS: 1 mi W of Santiago, *Tyson 5166* (MO).

5. **Senecio cooperi** Greenman, Publ. Field Columbian Mus., Bot. Ser. 2: 284. 1907. TYPE: Costa Rica, Cartago, *Cooper 5803* (GH, not seen).—FIG. 99.

Coarse *herb* with turgid, pithy stems, (1–)2–3 m tall, the uppermost internodes and branches in the inflorescence scabrous-pilose with dark-tipped hairs, at least some of which are glandular. *Leaves* alternate; blades 10–40 cm long,

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FIGURE 99. *Senecio cooperi* Greenman—A. Leaf (× ½).—B. Inflorescence (× ½).—C. Head (× 5⅖).—D. Floret (× 5⅖). [After *Allen 1459* (MO).]

A
B
PRA.
C
PM
D
PRA.

(5–)10–20 cm wide, about twice as long as wide; well-developed leaves elliptic to broadly lanceolate or oblanceolate, the largest subpandurate, tapering or abruptly contracted, the margin serrate-dentate with callose-denticulate teeth 4–5 mm apart, pinnately veined; petiole ca. ½ as long as the blade, prominently winged, the wing irregularly undulate, amplexicaul at the base; lower leaves glabrescent, but with lower surfaces scattered villous, especially on the veins; uppermost leaves becoming lanceolate subsessile bracts 10–20 cm long. *Inflorescence* a series of open, compound corymbiform to paniculate cymes, with 30–60(–200) heads, arising terminally and from the axils of upper leaves. *Heads* distinctly cylindrical and spreading only slightly in age, yellow or yellow-orange, radiate and fragrant; principal involucral bracts about 8, linear oblong, 8–10 mm long, 1 mm wide, the margins prominently scarious, erose at the apex; calyculate bracts 1–3, inconspicuous; receptacle flat with a few short scarious paleas irregularly interspersed among the achenes; ray florets ca. 5–8, thin and narrow, the tube 6–8 mm long, subfiliform, the ligule disposed at a right angle to the involucre but becoming lax in age, ca. 10 mm long and 1 mm wide in dried specimens; disc florets 10–18, exserted 4–6 mm beyond the involucre, the tube slender, 8–10 mm long, the limb funnelform, 3–5 mm long, deeply 5-lobed. *Achene* pubescent, narrowly fusiform to suburceolate, terete, 2–3 mm long, only occasionally filled and therefore presumably of low fertility; pappus of white, uniseriate, capillary bristles.

Senecio cooperi occurs in clearings, steep slopes, and disturbed sites in forested areas, mostly above 2,000 m, in the mountains of Chiriquí and adjacent Bocas del Toro. Apparently flowering the year round, the species has been most often collected in July, August, and September.

BOCAS DEL TORO: N slopes Cerro Horqueta, *Allen 4999* (US). CHIRIQUÍ: Trail from Cerro Punta to headwaters of Río Caldera, *Allen 1452* (NY, US). Cerro Punta, *Blum et al. 2425* (MO). Between Bambito and Cerro Punta, *Croat 10535* (MO, NY). NW Nueva Surina, *Croat 13530* (MO, NY). NW side of Cerro Pando, *Croat 15947* (MO). W of Cerro Punta, *Croat 22419* (MO). Above Cerro Punta, *D'Arcy 5351* (MO). La Popa, above Boquete, *D'Arcy & D'Arcy 6406* (MO). Cerro Punta, *D'Arcy & D'Arcy 6525* (MO). Cerro Pando, *D'Arcy & D'Arcy 6639* (MO). Bajo Chorro, Boquete, *Davidson 236* (MO, US). Cerro Horqueta, *Dwyer et al. 432* (MO, US). Boquete, *Dwyer 6997* (MO). Cerro Punta, *Gentry 5867* (MO); *King 3303* (US). Cerro Horqueta, *Maurice 864* (MO, US). Nueva California, *Tyson 6687* (MO). Finca Lérida, *Woodson & Schery 231* (MO). Near Bajo Mona and Quebrada Chiquera, *Woodson & Schery 515* (MO). Bajo Mona, *Woodson et al. 1014* (MO, NY).

6. **Senecio heterogamus** Hemsley, Biol. Centr. Am., Bot. 2: 242. 1881. TYPE: Costa Rica, *Örsted 192* (K, not seen).

Roldana heterogama (Hemsl.) H. Robinson & Brettell, Phytologia 27: 420. 1973.

Low *subshrub* 20–40 cm tall; stems coarse, distichous, branching; caudex woody, fibrous-rooted, 2–3 cm across, 2–5 cm long; pubescence lightly villous-pilose, at least some of the hairs glandular, especially on the upper stems and peduncles. *Leaves* alternate, about evenly distributed along the stem, 2.5–6 cm long, 2–7 cm wide, usually slightly wider than long, often eccentrically peltate, deltoid-orbicular to suborbicular with 5–9(–13) shallow lobes, denticulate with small but prominent teeth, palmately veined; petiole distinct, attached ca. 1 cm

inward from the margin, or sometimes basally, nearly as long as the blade or a little longer, basally expanded and sometimes subclasping; uppermost leaves reduced to lanceolate bracts. *Inflorescence* arising terminally, an open paniculate cyme with 5–20 heads. *Heads* yellow, disciform; involucral bracts ca. 13, narrowly lanceolate, 7–9 mm long; calyculate bracts 1–2, linear-subulate, 2–4 mm long, inconspicuous; ray florets 8–10, apparently fertile, the corolla tubular, ca. 5 mm long; disc florets 10–20, the tube narrow, 3 mm long, the limb conspicuously expanded, 5 mm long. *Achene* columnar to weakly fusiform, glabrous, to 4 mm long; pappus a single series of white capillary bristles equalling or slightly exceeding the involucre.

This species occurs at elevations above 2,000 m in the mountains of Chiriquí Province. In Panama it has been collected flowering in June and July, but most collections from elsewhere in Central America have been taken in December-April.

CHIRIQUÍ: Volcán de Chiriquí, *Woodson et al. 857* (MO).

7. **Senecio megaphyllus** Greenman, Publ. Field Columbian Mus., Bot. Ser. 2: 284. 1907. TYPE: Costa Rica, "Bords du Paraita Grande au Copey," *Tonduz 11700* (GH, not seen).

Coarse suffrutescent *herb* or *shrub*, 1–3 m tall, glabrate at maturity but with irregularly scattered arachnoid-villous tomentum, especially in and near the axils of the leaves. *Leaves* alternate, blade of well-developed upper leaves 8–15 cm long, 3–6 cm wide, about twice as long as wide, oblanceolate to elliptic, tapering serrate-dentate, the teeth callose-denticulate, pinnately veined; petiole winged, ca. ⅓ as long as the blade, weakly clasping at the base; uppermost leaves reduced to lanceolate, subsessile, subentire bracts, 3–5 cm long. *Inflorescence* a dense compound of several clustered corymbiform cymes arising terminally and in axils of the uppermost leaves, 10–20 cm across, the heads 40–60. *Heads* yellow-orange to orange; principal involucral bracts ca. 8, lanceolate to spatulate, scarious margined, tapering to a fimbriate tip, 6–7 mm long; calyculate bracts 2–4, linear, 3–4 mm long; receptacle flat with short, obscure, irregular scarious paleas less than 1 mm long; ray florets ca. 5, the tube 5–6 mm long, filiform, the ligule 5–8 mm long, 1 mm wide in dried specimens; disc florets 8–14, exceeding the involucre by 3–5 mm, the tube 6–8 mm long, the limb sharply distinct, 4 mm long, prominently lobed with sinuses ca. 2 mm deep, the style branches surmounted by a minute conical tuft of hairs. *Achene* broadly fusiform to columnar, glabrous, 2 mm long; pappus of white, capillary bristles in a single series, only slightly exceeding the involucral bracts.

This species occurs at high elevations, over 3,000 m, in the mountains of Chiriquí Province. It flowers in February and March.

A curious single specimen, *Stern et al. 1065*, is tentatively referred here, pending acquisition of more complete materials. The specimen is immature so positive identification is not possible, but the collectors refer to it as a "small tree, up to 8″ dia." Furthermore, it was collected at an elevation below that expected for S. *megaphyllus*. It may represent an undescribed entity.

CHIRIQUÍ: E of Boquete, Palo Alto, 5000 ft, *Stern et al. 1065* (MO). Volcán de Chiriquí, *Terry 1305* (MO). W slope of El Barú, *Tyson & Loftin 6142* (MO).

8. **Senecio oerstedianus** Benth. in Örst., Vidensk. Meddel. Dansk Naturhist. Foren. Kjøbenhavn 109. 1852. TYPE: Costa Rica, *Örsted* (not seen).—FIG. 100.

Erect *herb*, 30–50 cm tall; stems arising singly (or loosely clustered?); rhizome coarse, creeping, 10–15 mm in diam.; pubescence densely white-lanate throughout except on the upper surface of leaves, which are early irregular-glabrate, on stems unevenly glabrescent. *Leaves* evenly distributed along the stem but reduced upwards, alternate, pinnately veined, thick and coriaceous, at least in dried specimens, the lower and middle leaves lanceolate to narrowly ovate, acuminate, tapering at the base, the margin serrate-dentate, edges of the teeth weakly revolute, the blades 6–10 cm long, 2–5 cm wide, about 2–2½ times longer than wide; petiole ½–⅓ as long as the blade, sheathing-clasping at the base. *Inflorescence* a single, terminal, congested to loose, paniculate to subcorymbiform cyme of 10–20 heads, supported by stout, densely lanate peduncles. *Heads* radiate, yellow; involucral bracts ca. 21, narrowly lanceolate-subulate, greenish, with narrow, scarious margins, minutely erose-tipped, conspicuously but unevenly lanate tomentose on the outer surface; calyculate bracts few, linear-subulate, less than 5 mm long; receptacle flat, naked; ray florets ca. 8, ligule 8–10 mm long, 1 mm or more wide in dried specimens; disc florets 20–30, the corolla 7–8 mm long, the tube and limb not sharply distinguished. *Achene* columnar, glabrous, 2–3 mm long; pappus of copious, white, capillary bristles, equalling or slightly exceeding the involucral bracts.

Known in Panama only from about 3,000 m on Volcán de Chiriquí, this species flowers from February to March.

The specimens *Pittier 3094* in MO and US have different localities on the printed labels: "Upper belt of Chiriquí Volcán, northern slope; 3000 to 3374 m" (MO); "around El Potrero Camp, Chiriquí Volcano; 2800 to 3000 m" (US). The specimens both represent the same entity.

CHIRIQUÍ: Chiriquí Volcano, *Pittier 3094* (MO, US). Volcán de Chiriquí, *Terry 1314* (MO).

9. **Senecio parasiticus** Schultz-Bip. ex Hemsley, Biol. Centr. Amer., Bot. 2: 244. 1881. TYPE: not seen.

Cacalia parasitica Schultz-Bip. ex Braun, Bot. Zeitung (Berlin) 15: 759. 1857, nom. nud.

Liana, often described as "succulent," loosely climbing to 10–15 m, glabrate but with scattered hairs irregularly disposed throughout, becoming short-pilose upwards, especially on branches and peduncles. *Leaves* evenly distributed along the stem, alternate; blades 3–7 cm long, 1.5–2.5 cm wide, ca. 3–4 times longer than

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FIGURE 100. *Senecio oerstedianus* Benth.—A. Habit (× ⅗). [After *Schery 448* (MO).]—B. Ray floret (× 2⅕).—C. Disc floret (× 2⅕). [After *Dwyer 684* (MO).]

A
B
C

wide, elliptic to obovate, acuminate, tapering to a distinct petiole, entire or sometimes revolute at the extreme edge, pinnately veined; petiole ⅓ as long as the blade. *Inflorescence* a series of small, corymbiform cymules with 8–12 heads each, arising terminally or in axils of the upper leaves. *Heads* white; involucral bracts 8, lanceolate, scarious margined, 6–7 mm long; calyculate bracts 1–2, inconspicuous, 1–2 mm long; receptacle slightly convex with prominent but minute, irregularly dentate paleas less than 1 mm long protruding between the achenes; ray florets 5, greatly reduced, the corolla ca. 5 mm long, either subactinomorphic and 5-lobed, or with a minute ligule less than 1 mm long; disc florets 8–10, the corolla 6–8 mm long, not sharply distinguished into a tube and limb. *Achene* apparently fusiform, glabrous, 1–2 mm long; pappus a single series of white, capillary bristles.

Senecio parasiticus occurs at elevations around 1,000 m in the mountains of Chiriquí, Bocas del Toro, and Veraguas Provinces. It has been collected flowering March, April, and May. A poorly understood, polymorphic complex in Panama and adjacent countries, it perhaps encompasses more than the one entity recognized here.

BOCAS DEL TORO: Divide on Chiriquicito-Caldera trail, *Kirkbride & Duke 977* (MO). CHIRIQUÍ: Chiriquí Viejo Valley, *White 111* (MO). VERAGUAS: W of Santa Fe on road past Escuela Agrícola Alto Piedra, *Liesner 920* (MO).

XI. CARDUEAE

ROBERT C. GARDNER[63]

Cardueae Cass., Jour. Phys. 88: 155. 1819. "Carduineae." TYPE: *Carduus* L.

Carlineae Cass., Jour. Phys. 88: 154. 1819. TYPE: *Carlina* L.
Centaureae Cass., Jour. Phys. 88: 154. 1819. TYPE: *Centaurea* L.
Echinopseae Cass., Jour. Phys. 88: 157. 1819. TYPE: *Echinops* L.
Cynareae Less., Linnaea 5: 128. 1830. TYPE: *Cynara* L.

100. CIRSIUM

Cirsium Miller, Gard. Dict., abr. ed. 4. 1754. TYPE: none cited.

Acaulescent *herb* to 4 dm tall; stems simple to several from the base. *Leaves* alternate, usually lobed, spines distributed along the margins, frequently decurrent on the stem. *Heads* discoid; involucre multiseriate, the bracts usually imbricate, often spine-tipped, sometimes with a glutinous dorsal ridge; receptacle subconic, bristly; florets perfect, the corolla white to purple, tubular, 5-cleft, the anthers

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appendaged, basally caudate with fringed auricles, the style with a thickened, often hairy ring below the branches, these connate except near the tip. *Achenes* oblong, somewhat flattened; pappus of plumose bristles.

Cirsium has been confused with two Old World genera: *Carduus* and *Cnicus*. *Carduus* has barbellate pappus bristles while *Cnicus* has a 2-seriate pappus, the inner series being shorter than the outer. *Cirsium* can be differentiated by its uniseriate, plumose pappus. About 200 species of *Cirsium* are native to the Northern Hemisphere and about 50 species are native to temperate America.

Besides the two species enumerated below, a third *Cirsium* species, *C. vulgare* (Savi) Airy-Shaw, has been seen from central Costa Rica (*Taylor 4463B*, NY). This additional taxon is an introduction from Europe, and in North America is widespread. Because of the weedy nature of *C. vulgare*, it is possible that further collecting will show that it occurs in Panama. *Cirsium vulgare* has decurrent leaves, as does *C. mexicanum*, but is easily distinguished by having reflexed involucral bracts and minute appressed spines on the upper leaf surfaces.

a. Leaf bases decurrent, forming wings on the stem; involucre of mature heads 3–3.5 cm tall; outer rows of involucral bracts with a glutinous dorsal ridge ..... 1. *C. mexicanum*
aa. Leaves clasping, not forming wings on the stem; involucre of mature heads 4.5–6 cm tall; none of the involucral bracts with a glutinous dorsal ridge ..... 2. *C. subcoriaceum*

1. **Cirsium mexicanum** DC., Prodr. 6: 636. 1837. TYPE: Mexico, Tamaulipas, around Tampico, 1826–1827, *Berlandier* (G, not seen).—FIG. 101.

Cnicus costaricensis Polak., Linnaea 41: 581. 1877. TYPE: Costa Rica, San José, *Polakowsky 64* (B, not seen, F, photo).
C. mexicanus (DC.) Hemsley, Biol. Centr. Amer., Bot. 2: 251. 1881.
Carduus mexicanus (DC.) E. L. Greene, Proc. Acad. Nat. Sci. Philadelphia 1892: 363. 1893.
Cirsium costaricensis (Polak.) Petrak, Beih. Bot. Centralbl. 27: 219. 1910.

Annual *herbs*, 10–40 dm tall; stems simple below, branching above, tomentose when young, the tomentum becoming floccose with age. Lower *leaves* to 45 cm long and 18 cm wide, the sinus depth to 95% of the leaf width; upper leaves to 10 cm long and 6 cm wide, the sinus depth variable and less than in the lower leaves; leaf bases decurrent, the wings to 5 cm long, tomentose beneath, glabrous above or with a thin tomentum along the major veins, the marginal spines 6–12 mm long, usually longest on decurrent wings. *Inflorescence* of terminal clusters of 3–5 or single heads on short peduncles arising from the axils of the upper and middle cauline leaves. *Heads* with the involucre 8- or 9-seriate, 3–3.5 cm tall, 1.5–2 cm in diam. at the base, the outer involucral bracts 4–6 mm long, basally 1–2 mm wide, with a glutinous dorsal ridge, tapering to a 5–7 mm long spine, the innermost bracts 25–35 mm long, 1–2 mm wide, tapering, twisted and often purple near the tip; corolla purple to reddish, 26–30 mm long, the lobes 4–5 mm long, the anthers colorless, 4–5 mm long, the style purple 27–31 mm long, the branches 2–3 mm long. *Achenes* 4–5 mm long, 1–1.5 mm in diam.; pappus 23–25 mm long.

This species flowers mainly from January through May (one specimen collected in August). The description is based mostly on Costa Rican plants.

CHIRIQUÍ: 20 km W of Puerto Armuelles, *Busey 541* (MO).

B
A
L. Mourrély

2. **Cirsium subcoriaceum** (Less.) Schultz-Bip. in Seem., Bot. Voy. Herald 312. 1856.

Carduus subcoriaceus Less., Linnaea 5: 130. 1830. TYPE: Mexico, "in monte Macultepec per. Jalapam," *Schiede & Deppe 265* (281 assigned herbarium number, HAL).
Cirsium heterolepis Benth., Pl. Hartw. 87. 1841. TYPE: Guatemala, "in montibus Mixco," *Hartweg 596* (K).
C. maximum Benth., Pl. Hartw. 289. 1848. TYPE: Mexico, "in montibus Santa Rosa," *Hartweg 1837* (K).
Cnicus heterolepis (Benth.) A. Gray, Proc. Amer. Acad. Arts 10: 44. 1874.
C. subcoriaceus (Less.) Hemsley, Biol. Centr. Amer., Bot. 2: 252. 1881.
C. pinnatisectus Klatt, Bot. Beibl. Leopoldina 1895: 8. 1895. TYPE: Costa Rica, "Paramos de l'adejonal," 1900 m, *Tonduz 7791* (GH).
Cirsium pinnatisectum (Klatt) Petrak, Beih. Bot. Centralbl. 27: 236. 1910.

Annual *herbs*, 10–40 cm tall; stems simple below, branching above, densely tomentose when young, the tomentum becoming floccose with age. Lower *leaves* to 40 cm long and 25 cm wide, the sinus depth to 90% of the leaf width; upper leaves to 25 cm long and 6 cm wide, less divided than the lower leaves; the leaf bases clasping, tomentose beneath, glabrous or with a thin tomentum above, the marginal spines 5–12 mm long, usually longest toward the base of the upper leaves. *Inflorescence* of terminal heads borne singly or in clusters. *Heads* with the involucre 8–19-seriate, 4.5–6 cm tall, 3–4 cm across the base, the outer involucral bracts 25–30 mm long, 4.5–5 mm wide at the base, tapering to a 4–5 mm long spine, spiny along the margin, without a glutinous dorsal ridge, arachnoid-pubescent along the margins, the innermost bracts 40–50 mm long, 1–3 mm wide, tapering and twisted near the tip, erose; corolla pale yellow, 43–53 mm long, the lobes 23–28 mm long, the anthers pink to yellow, 13–16 mm long, the style purple, 53–65 mm long, the branches 2–2.5 mm long. *Achenes* 5–7 mm long, 2 mm in diam.; pappus 28–33 mm long.

This species usually flowers from January through March (one specimen collected in June). The description here is based mainly on Costa Rican plants.

It is possible that the earliest correct name for this taxon is *Cirsium cernuum* Lag., Gen. Sp. Pl. Nov. 24. 1816. The original description, although short, suggests specimens examined. This thistle was described from cultivated material grown at the Jardín Botánico, Madrid, but type material has not been located.

CHIRIQUÍ: Upper valley of Río Chiriquí Viejo, *Allen 1588* (MO). 2.7 mi NW of Río Chiriquí Viejo, W of Cerro Punta, *Croat 22352* (MO). Volcán de Chiriquí, *Woodson & Schery 467* (MO). Cerro Punta, *Blaisdell 358* (FSU).

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FIGURE 101. *Cirsium mexicanum* DC.—A. Habit (× ⅖).—B. Floret (× 1½). [After *Busey 541* (MO).]

XII. MUTISIEAE

BERYL BRINTNALL SIMPSON[64]

Mutisieae Cass., Jour. Phys. 88: 199. 1819. TYPE: *Mutisia* L.f.

Nassauvieae Cass., Jour. Phys. 88: 198. 1819. TYPE: *Nassauvia* A. L. Juss.
Onoserideae H.B.K., Nov. Gen. Sp. Pl. 4: 4. 1820 (ed. fol. 1818). TYPE: *Onoseris* DC.
Chaetanthereae Dumort., Anal. Fam. Pl. 31. 1829, nom. illeg. consist., superfluous when published. TYPE: *Chaetanthera* Ruiz & Pavon.

Herbs, *shrubs* or *vines*. *Leaves* alternate or basal. *Inflorescence* paniculate, corymbose or a solitary head. *Heads* homomorphic (discoid) or heteromorphic (disciform or radiate), female, functionally male, or hermaphroditic; involucral bracts in few to several series, imbricate; receptacle flat or convex, naked, foveolate, fimbrillate, paleaceous or glandular; corolla bilabiate with a 3-parted outer ligule and 2, 1, or no inner lobes, or tubular and equally 5-parted; anthers with an undemarcated, pointed terminal appendage, and usually basal auricles or pointed tails, these sometimes fringed at the tips; style branches relatively short, truncate, or rounded. *Achenes* various, columnar or fusiform, ribbed or smooth, glabrous or pubescent; pappus of setose, plumose, or flat bristles, sometimes fine.

The Mutisieae is a predominantly South American tribe with a few genera extending through Central America and the West Indian Islands to North America, and in Asia, Africa, Australia, and the Hawaiian Islands.

Literature:

Jeffrey, C. 1967. Notes on Compositae: II. The Mutisieae in east tropical Africa. Kew Bull. 21: 177–223.

a. Heads heterogamous (with female ray florets, and hermaphroditic, or hermaphroditic combined with functionally male and/or female central florets) or completely unisexual (plants dioecious).
  b. Subshrubs or vines; plants monoecious or dioecious; heads borne on leafy branches, turbinate or scapose (Gochnatiinae).
    c. Plants dioecious; heads borne singly on branches, broadly campanulate in outline; involucral bracts ovate to lanceolate, stiff, with a few scattered hairs; achenes glabrous ..... 104. *Lycoseris*
    cc. Plants monoecious; heads borne in panicles, narrowly turbinate in outline; involucral bracts linear-lanceolate, soft, lanate; achenes strigose ..... 105. *Onoseris*
  bb. Rosette herbs; plants monoecious; heads borne singly on scapes (Mutisiinae).
    d. Leaves with scattered strigose hairs on both sides; achenes truncate; external female florets with staminodes and corollas with a long (± 10 mm) strap-shaped ligule ..... 102. *Gerbera*
    dd. Leaves densely white lanate beneath, glabrate above; achenes with a long beak; external female florets lacking staminodes and corollas with a short (less than 5 mm) ligule ..... 101. *Chaptalia*
aa. Heads monogamous, all flowers alike, perfect (Nassauviinae).

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e. Plants glabrate; heads narrow, turbinate; receptacle naked; pappus of several rows of setose bristles; corollas yellow ..... 106. *Trixis*
ee. Plants with a rust-colored tomentum, especially on the stems, leaf undersides, and bracts; heads hemispherical; receptacle with paleas enclosing the florets; pappus of a single series of setose bristles; corollas white ..... 103. *Jungia*

101. CHAPTALIA

Chaptalia Vent., Descr. Pl. Jard. Cels. *pl. 61.* 1802. TYPE: *C. tomentosa* Vent.

Leria DC., Ann. Mus. Natl. Hist. Nat. 19: 68. 1812. TYPE: *L. nutans* (L.) DC., based on *Tussilago nutans* L. = *Chaptalia nutans* (L.) Polak.
Lieberkuhna Cass., Dict. Sci. Nat. 26: 286. 1823. TYPE: *L. bracteata* Cass., nom. illeg. = *Chaptalia piloselloides* (Vahl) Baker.
Loxodon Cass., Dict. Sci. Nat. 27: 253. 1823. TYPE: *L. brevipes* Cass., nom. illeg. = *Chaptalia exscapa* (Pers.) Baker.
Oxydon Less., Linnaea 5: 357. 1830. TYPE: *Oxydon bicolor* (H.B.K.) Less., nom. illeg. based on *Chaptalia runcinata* H.B.K.
Thyrsanthema Kuntze, Rev. Gen. Pl. 1: 369. 1891, based on *Chaptalia nutans* (L.) Polak.

Herbs with monocephalous, more or less scapose, lanate flowering stems. *Leaves* in a basal rosette, lanceolate to runcinate, entire, toothed or lobed, lanate to various degrees beneath and occasionally above. *Heads* inconspicuously radiate, turbinate or campanulate; involucre of several series of linear-lanceolate, acute bracts increasing in size inwards, lanate on the outer surfaces; receptacles flat, foveolate; florets trimorphic, occasionally only dimorphic; outermost 1 to several rows of florets female, ligulate, the ligule strap-shaped, more or less tridentate, with or without 1 or 2 minute teeth in the inner part; intermediate series of florets (sometimes wanting) also female, the corolla tubular, shorter than the style; central florets perfect with bilabiate corollas, the outer lip 3-parted, the inner lip 2-parted, the anthers with entire tails, the style short, rounded, hairy. *Achenes* columnar to fusiform, beaked or beakless, 5–several-nerved, glabrous or villous; pappus of copious, tawny, white or pinkish, setose bristles. *Pollen* spherical or prolate, tricolporate, reticulate.

The genus *Chaptalia* contains about 35 species in 5 sections (Burkart, 1944). The generic limits between *Chaptalia*, *Gerbera*, and *Triocline* are somewhat vague and problems of circumscription have been discussed by Jeffrey (1967). Within *Chaptalia* itself, many specimens seem to intergrade between species. The fact that fertile artificial hybrids have been readily made between several of the species indicates that there is relatively little genetic divergence between various recognized taxa.

Literature:

Burkart, A. 1944. Estudio del género de compuestas *Chaptalia*. Darwiniana 6: 505–594.

a. Scape bractless; leaves lyrate; heads nodding when young and at fruit maturity ..... 1. *C. nutans*
aa. Scapes with scalelike bracts near the heads; leaves lanceolate; heads always upright ..... 2. *C. runcinata*

1. **Chaptalia nutans** (L.) Polak., Linnaea 41: 582. 1878.—FIG. 102.

Tussilago nutans L., Syst. Nat. 10(2): 1214. 1759. TYPE: America, collector unknown, Herb. Linn. 995.5 (LINN, not seen; US, microfiche).
T. lyrata Pers., Syn. Pl. 2: 456. 1807. TYPE: Hab. in Amer. Meridionali (not located).
Leria nutans (L.) DC., Ann. Mus. Natl. Hist. Nat. 19: 68. 1812.
L. lyrata Cass., Dict. Sci. Nat. 26: 102. 1823. TYPE: not located.
Tussilago vaccina Vell., Fl. Flum. Icon. 8: 143. 1831. LECTOTYPE: Fl. Flum. Icon.: *icon. 143.*
Gerbera nutans (L.) Schultz-Bip. in Seem., Bot. Voy. Herald 313. 1856.
Thyrsanthema nutans (L.) Kuntze, Rev. Gen. Pl. 1: 369. 1891.
Chaptalia carduacea E. L. Greene, Leafl. Bot. Observ. Crit. 1: 191. 1906. TYPE: U.S.A., Texas, San Diego, 1884–1888, *Croft 35* (US, holotype).
C. leonina E. L. Greene, Leafl. Bot. Observ. Crit. 1: 193. 1906. TYPE: Mexico, States of Coahuila and Nuevo Leon, Feb.–Oct. 1880, *Palmer 764* (US, holotype).
C. diversifolia E. L. Greene, Leafl. Bot. Observ. Crit. 1: 194. 1906. TYPE: Guatemala, vicinity of Mazatenango, 350 m, 20 Feb. 1905, *Maxon & Hay 3504* (US, holotype).
C. subcordata E. L. Greene, Leafl. Bot. Observ. Crit. 1: 195. 1906. TYPE: St. Croix, Big Fountain Garden, 24 June 1896. *Ricksecker 447* (US, holotype).
C. erosa E. L. Greene, Leafl. Bot. Observ. Crit. 1: 196. 1906. TYPE: Costa Rica, San José, road edges, 1135 m, June 1892, *Tonduz 447* (US, holotype).
C. majuscula E. L. Greene, Leafl. Bot. Observ. Crit. 1: 196. 1906. TYPE: Bolivia,, Maipiri, 5000 ft, May 1886, *Rusby 1677* (US, holotype).
C. texana E. L. Greene, Leafl. Bot. Observ. Crit. 1: 191. 1906. TYPE: U.S.A., Texas, sparsely wooded ground in western Texas, *Neally 297* (US, holotype).
C. nutans var. *texana* (E. L. Greene) Burkart, Darwiniana 6: 569. 1944.

Perennial scapose *herbs* 46–87 cm tall. *Leaves* in a basal rosette, lyrate, the terminal segment comprising half or more of the leaf, lobed, acute, tapering at the base, 3–10 cm wide, 9–34 cm long, glabrous or with patches of wooly trichomes above, densely lanate beneath, stem leaves lacking. *Heads* inconspicuously radiate, borne singly, often several per plant, turbinate, nodding when young and at fruit maturity, to 4 cm long and 6 cm wide; involucral bracts linear, lanceolate, imbricate in several unequal series, the margins entire, the tips red, acute, densely lanate on the outer surface; receptacle flat, foveolate; florets trimorphic, white; outer series of florets female with ligulate corollas, the ligule narrow, strap-shaped, ca. 12 mm long, extending only slightly beyond the involucral bracts; second series of florets female, the corolla tube of varying length, shorter than the style; innermost disc florets perfect, the corollas bilabiate. *Achenes* fusiform, reddish brown or green, with 5–8 white nerves, beaked, the beak forming over half the length, 0.5–1.5 mm long, glabrous or slightly pilose; pappus 12–15 mm long, of tawny or more often pink, capillary bristles. Chromosome number $2n = 48$ (Federov, 1969).

Chaptalia nutans is an extremely widespread and variable species ranging from the United States to Argentina, and in the West Indies. Plants from various populations, or even within one population, can flower with scapes ranging from 6 cm to 1 m tall. The species may be recognized by the orientation of the heads; when immature or as the achenes are shed they are nodding but at anthesis they are upright. It is distinguished from *C. runcinata* by its bractless scape and lyrate, lobed leaves. Leaves of this species wetted with oil were applied medicinally in northern Argentina according to Burkart (1944).

BOCAS DEL TORO: At Bocas, *Lazer et al. 2449* (FSU). Changuinola to 5 mi S at the Junction of Ríos Changuinola and Terebé, 100–200 ft, *Lewis et al. 917* (MO). CANAL ZONE:

FIGURE 102. *Chaptalia nutans* (L.) Polak.—A. Habit (× ½).—B. Central floret (× 6). [After *Lewis et al.* 1639 (MO).]

Summit Garden, *D'Arcy & D'Arcy 6187* (MO). Between Madden Dam and Saddle II near Alahuela, 90–100 m, *Dodge et al. 16501, 16512* (both MO). Ancón Hill, *Greenman & Greenman 5116* (MO). Fort Clayton, *Tyson 1840* (MO). Cerro Azul, 2000 ft, *Tyson 2068* (MO). Cerro Jefe, *Tyson et al. 4310* (MO). Miraflores Lake, *White & White 191* (MO). BARRO COLORADO ISLAND: *Ebinger 134* (MO); *Shattuck 157, 199* (both MO); *Netting 22* (MO); *Croat 4087a, 6537, 6903, 13498* (all MO). CHIRIQUÍ: 25 km W of Puerto Armuelles, 400–600 m, *Busey 533* (MO). Boquete, 3800 ft, *Davidson 640* (MO). Boquete, 5500 ft, *Dwyer 7013* (MO). Llanos del Volcán, 1120–1200 m, *Seibert 337* (MO). Near Boquete, 1200–1500 m, *Woodson & Schery 774* (MO). COCLÉ: Vic. of El Valle, 600–1000 m, *Allen 1162* (MO). COLÓN: Vic. of Sardinilla, *Blum & Tyson 488* (FSU, MO). DARIÉN: Vic. of Boca de Cupe, 40 m, *Allen 895* (MO). HERRERA: 12.5 mi S of Ocú, 1200 ft, *Lewis et al. 1639* (MO). LOS SANTOS: Loma Prieta, 800–900 m, *Duke 11875* (MO). 25 mi SW of Tonosí, 2500–3000 ft, *Lewis et al. 2884* (MO). PANAMÁ: Ville Guadelupe-Calle, *de Hoyos 25* (MO). Pan-Am Hwy. near Jenené, Río Cañita, *Duke 3822* (MO). Toward top of Cerro Campana, *Duke 5972* (MO). Goofy Lake to 8 mi S of Goofy Lake, *Dwyer 7056* (MO). Near Arraiján, *Woodson et al. 1347* (MO). SAN BLAS: Without locality, *Duke 10129* (MO).

2. **Chaptalia runcinata** H.B.K., Nov. Gen. Sp. Pl. 4: 4 *tab. 303.* 1820 (ed. fol. 1818). TYPE: Colombia, Smita River, Oct. *Humboldt & Bonpland* (not seen).

Loxodon longipes Cass., Dict. Sci. Nat. 27: 255. 1823, nom. illeg., superfluous when published.
Oxydon bicolor Less., Linnaea 5: 357. 1830, nom. illeg., superfluous when published.

Acaulescent perennial *herb* to 9 cm tall. *Leaves* all basal, oblanceolate, acute, retrorsely dentate with mucronate teeth, tapering to the base, 30–52 mm long, 11–13 mm wide, glabrous above, densely white lanate beneath. *Inflorescence* a monocephalous scape, 50–100 mm tall, lightly lanate, with narrow, scalelike bracts near the apex. *Heads* discoid, turbinate, 10 mm wide, 12 mm long, several per plant; involucral bracts in several series increasing in size inwards, linear-lanceolate, acute, entire, soft, glabrous or with a few scattered trichomes; receptacle slightly convex, foveolate; florets not exceeding the rim of the involucre, trimorphic; outer series of florets female, the corolla ligulate with a strap-shaped, 4-dentate ligule and no inner tooth, without anthers; second series of florets female, the corolla tubular, irregularly lobed, extending half way up the style, the style branches glabrous, spreading; innermost disc florets perfect, the corolla more or less 5-dentate but with 2 of the teeth set apart from the others by deeper sinuses, the style short, pubescent. *Achenes* beaked, ribbed, grey-green, glabrous; pappus yellow, of setose bristles.

Records of *Chaptalia runcinata* are rare for Panama, but the species has an extensive distribution elsewhere ranging from Costa Rica east into northern South America, south across Bolivia and Paraguay, and into central Argentina. This species is distinguished from *C. nutans* by the numerous bracts along the flowering stem and the nonpetiolate, retrorsely dentate leaves. Burkart (1944) reported that in Argentina *C. runcinata* produces during the year first a succession of cleistogamous and chasmogamous heads, and then a second set of cleistogamous heads. Burkart interpreted the behavior in Argentina as an adaptation to environmental conditions in the Pampas. It is not known if Panamanian plants also produce cleistogamous heads. The only specimen seen has chasmogamous heads.

CHIRIQUÍ: Llanos Francia, 3300 ft, *Stern et al. 1189* (MO).

102. GERBERA

Gerbera[65] L., Opera Varia (Soulsby no. 9) 247. 1758, nom. cons. TYPE: *G. linnaei* Cass., Dict. Sci. Nat. 18: 460. 1820. "*Gerberia*." (= *Arnica gerbera* L.), typ. cons.

Rosette *herbs* with bracteate or ebracteate flowering stems. Basal *leaves* lanceolate, ovate or lyrately parted, usually pubescent on both surfaces, petiolate. *Heads* radiate (Panama), solitary; involucre turbinate or campanulate, of several series of imbricate bracts, the outer series usually dorsally pubescent; florets of the usually single outer series female, the corolla bilabiate with a long, 3-dentate ligule and 2 filiform inner segments, staminodes present (or functional stamens, if the heads are homogamous); inner disc florets perfect, the corollas bilabiate, shorter than those of the outer series, the anthers with long, lacerate basal appendages, the style branches linear, slightly flattened, obtuse. *Achenes* with a short beak or truncate, slightly flattened, ribbed, glabrous or with strigose or villous pubescence; pappus of abundant, setose or capillary bristles.

1. **Gerbera jamesonii** Bolus, Gard. Chron., ser. 3, 5: 772, *fig. 122*. June 1889. TYPE: a cultivated plant in the alpine house of Kew Gardens, seeds originally sent from Natal (not seen).

Robust, perennial, rosette *herb* ca. 40 cm tall arising from a sericeous caudex. Basal *leaves* lyrately parted, the segments irregularly dentate, to 17 cm long and 4 cm wide, petiolate, the upper and lower surfaces with scattered strigose trichomes, petiole ca. ½ the length of the leaf. *Inflorescence* a monocephalous scape, stout, ebracteate with scattered strigose hairs and narrowing slightly under the head. *Heads* radiate, ca. 3 cm wide and 5 cm long; involucre of 2–3 series of lanceolate, entire, acute bracts, the outer series setose on the back, the inner series slightly scarious along the margins and glabrate; receptacle convex, naked; outer florets female, the corollas ca. 25 mm long with a 3-dentate, strap-shaped ligule ca. 10 mm long and 2 filiform, shorter, inner segments, the ligules yellow on the underside, orange above; disc florets perfect, the corollas bilabiate, ca. 10 mm long, the outer lip entire or irregularly dentate, recurved, the inner lip of two slightly shorter, filiform segments, orange-yellow, glabrous. *Achenes* fusiform, truncate when immature but with a very short beak when mature, ribbed, light brown, covered with strigose trichomes: pappus of copious, blond, setose bristles.

Gerbera jamesonii is a native of Africa and is widely cultivated. In Panama it is cultivated and apparently has not escaped into the wild. It rarely fruits in cultivation.

CHIRIQUÍ: Cultivated in a nursery in Boquete, 3600 ft, *D'Arcy & D'Arcy 6511* (MO).

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[65] Not only is the nomenclature of *Gerbera* confused, but the generic limits of the genus are still unclear. Jeffrey (1967: 211–214) discussed the alternative circumscriptions of the genus and what he considers to be natural groupings of species within the complex. It should be noted that because of the subsequent conservation of the name *Gerbera* the author of the genus and the type given by Jeffrey (different from above) are now incorrect. Since *Gerbera* is introduced and only cultivated in Panama, complete synonymy, given by Jeffrey, is not repeated.

103. JUNGIA

Jungia L.f., Suppl. Pl. 58. 1781. TYPE: *J. ferruginea* L.f.

Trinacte Gaertn., Fruct. 2: 415. 1791, nom. illeg., superfluous when published. TYPE: *T. ferruginea* (L.f.) Gaertn.

Rhinactina Willd., Ges. Naturf. Freunde Berlin Mag. Neuesten Entdeck. Gesammten Naturk. 1: 139. 1807. TYPE: *R. cinerarioides* Willd. ex Less., nom. nud. Cited by Lessing as a herbarium name in synonymy under *Jungia ferruginea*.

Dumerilia DC., Ann. Mus. Natl. Hist. Nat. 19: 71. *tab. 15, 16.* 1812. TYPE: *D. axillaris* DC.

Pleocarpus D. Don, Trans. Linn. Soc. London 16: 228. 1830. TYPE: *P. revolutus* D. Don.

Climbing, caulescent *herbs* and *shrubs* 60 cm to 30 m long; stems densely pubescent to glabrescent. *Leaves* alternate, petiolate, palmately to pinnately veined, mostly semicoriaceous, decreasing in size toward the clusters of heads. *Inflorescences* axillary or terminal panicles or corymbs. *Heads* discoid; involucre campanulate or cylindrical, the bracts in 2 series, the innermost often encircling the outer florets; receptacle paleaceous and/or fimbrillate; florets zygomorphic, the corolla bilabiate, with the outer lip 3-dentate and with 2 shorter inner teeth, the anthers with elongate, auriculate basal appendages and an elongated terminal portion, the style branches truncate. *Achenes* cylindrical or tetragonal, truncate or slightly beaked, glabrous or pubescent; pappus of 1 or 2 series of setose to almost plumose bristles. *Pollen* tricolporate with conspicuous ridges along the colpi, exine reticulate.

Jungia is a distinctive genus, even in the closely knit Nassauviinae. Its homogamous heads of bilabiate corollas and truncate style branches place it in this subtribe, but it is the only viny member of this subtribe. The genus appears most closely related to *Trixis* from which it differs in having species with white florets (except the one species *Jungia revoluta* (D. Don) Reiche formerly placed in *Pleocarpus*), in having a uniseriate pappus, and in having an unusual covering of dense strigose trichomes. The 30 species in the genus range from Mexico through Central America and along the Andes to Argentina and Chile. The primary development of the genus has been in Peru.

Literature:

Cerrate Valenzuela, E. 1951. Revisión de las especies peruanas del género *Jungia*. Publ. Mus. Hist. Nat. "Javier Prado", Ser. B., Bot. 4: 1–24.

1. **Jungia ferruginea** L.f., Suppl. Pl. 390. 1781. TYPE: America (not seen).—FIG. 103.

Dumerilia paniculata DC., Ann. Mus. Natl. Hist. Nat. 19: 72, *tab. 16.* 1812. TYPE: Peru, *de Jussieu* (P, not seen; US, photo from Paris Herbarium #38156).

Vine reaching 30 m in length while climbing among trees; stems with dense brown strigose trichomes. *Leaves* alternate, 3.7–11.4 cm wide, 6.0–13.0 cm long, palmately lobed, usually with 5–7 lobes, both sides with dense, dark strigose trichomes; petiole to 5 cm long. *Inflorescence* of numerous heads in axillary panicles. *Heads* discoid, campanulate, to 5 mm tall; involucre of 2 series of ovate

FIGURE 103. *Jungia ferruginea* L.f. Habit (× ½). [After *Skutch* 3622, Costa Rica (MO).]

to lanceolate, acute, entire bracts with strigose trichomes on the outer face, the outer series reduced, the inner series alike, few, surrounding the outermost florets; receptacle with a tuft of hairs in the center; florets few, 6–8 per head, white, all perfect, the corollas bilabiate, the outer lip 3-dentate and the inner lip of 2 small recurved equal segments, glabrous or slightly pubescent. *Achenes* fusiform, beakless, glabrous and slightly striate; pappus white, a single series of soft, setose, almost plumose bristles.

CHIRIQUÍ: Cerro Punta, 2000 m, *Allen 1520* (GH, MO). Chiquero, 6500 ft, *Davidson 559* (GH, MO). PANAMÁ: Cerro Punta, ca. 7000 ft, *Blaisell 379* (FSU).

104. LYCOSERIS

Lycoseris Cass., Dict. Sci. Nat. 33: 474. 1824. TYPE: *L. mexicana* (L.f.) Cass.

Diazeuxis D. Don, Trans. Linn. Soc. Lond. 16: 251. 1830. TYPE: *D. trinervis* D. Don.

Dioecious *shrubs* (or vines). *Leaves* alternate, short-pedunculate (or sessile), lanceolate, tomentose beneath. *Inflorescences* terminal, solitary, sometimes clustered heads. *Heads* disciform or radiate, the male heads larger than the female; involucres campanulate to globose, the bracts stiff, lanceolate to ovate, entire, acute, in many series; receptacles flat, naked or fimbrillate; male heads with ligulate, 2–3-toothed marginal florets and tubular 5-parted or bilabiate disc florets, the corolla orange, the anthers with long, entire basal appendages, the style branches connate, the ovaries all rudimentary, sterile, the pappus a single series of white bristles; female heads with a row of ray florets, the corolla with a 3-parted ligule and 1 small (or no) inner tooth, the ovary functional, the disc florets numerous, the corolla orange, tubular, narrow, 5-dentate, the style branches thin, long, spreading, the androecium sometimes present and functional, the ovary functional. *Achenes* columnar, glabrate; pappus of numerous fine setose bristles.

The genus contains about 15 species that extend from Bolivia northward, primarily in the Andes, to Central America as far as Guatemala.

Literature:

Johnston, I. M. 1949. Compositae. *In* The Botany of San Jose Island. Sargentia 8: 288–296.

1. **Lycoseris latifolia** (D. Don) Benth., Bot. Voy. Sulphur 121. 1845.—FIG. 104.

Diazeuxis latifolia D. Don, Trans. Linn. Soc. Lond. 16: 302. 1830. TYPE: Venezuela, near Caracas, *Fanning* (not seen).

Carduus cernuus Bertol., Fl. Guatemala. 431. 1840. TYPE: Guatemala, Volcán d'Acqua, *Velasquez* (not seen). (A female plant in fruit.)

Aster crocatus Bertol., Fl. Guatemala 434. 1840. TYPE: Guatemala, Volcán d'Acqua, *Velasquez* (not seen). (A male plant.)

Lycoseris squarrosa Benth., Bot. Voy. Sulphur 121. 1845. TYPE: Panama, Gulf of Fonseca, Nicoya, *Hooker* (not seen).

L. crocata (Bertol.) Blake, Bull. Torrey Bot. Club 53: 218. 1926.

L. oblongifolia Rusby, Descr. S. Amer. Pl. 162: 120. 1920. TYPE: Colombia, *Smith 661* (US).

FIGURE 104. *Lycoseris latifolia* (D. Don) Benth.—A. Female plant, habit (× ⅓).—B. Disc floret, female (× 2).—C. Achene (× 2⅗). [After *Cisneros 26* (MO).]—D. Male plant, habit, (× ⅓).—E. Anther (× 2½).—F. Outer floret (× 2½).—G. Inner, male floret (× 2½). [After *Croat* 8979 (MO).]

Woody, branched, dioecious, scrambling *shrub* to 5 m tall; stems terete, tomentose when young, glabrescent. *Leaves* alternate, lanceolate, entire or inconspicuously serrate, acuminate, trinerved, shortly pedunculate, 18–43 mm wide, 110–180 mm long. *Inflorescences* of solitary, terminal, many-flowered heads. *Heads* of 2 kinds; involucres of many imbricate series of ovate to lanceolate, entire, acuminate bracts often with the tips recurved; receptacles flat, naked; male heads ca. 35 mm wide and 25 mm long, the outer florets orange, to 15 mm long, the corolla ligulate, 2–3-dentate, the anthers lacking, the style and ovary nonfunctional, the disc florets with the corolla tubular, 5-parted, regular, ca. 15 mm long, the anthers functional, the ovary sterile; female heads orange, to 80 mm wide and 60 mm long, the corolla of the outer florets often bilabiate, the outer lip 3-parted and the inner lip lacking or filiform, the style ca. 23 mm long, the ovary sterile, the disc florets narrowly tubular, 5-dentate, ca. 23 mm long, the anthers lacking, the ovary fertile. *Achenes* columnar, slightly constricted apically,

glabrous, to 12 mm long, deep red-brown; pappus white, of numerous soft capillary bristles to 2.5 cm long.

Lycoseris latifolia is a widespread species ranging from Guatemala through Venezuela and Colombia. The striking difference in size between the female and male heads led Bertolini to describe the female plant as a thistle (*Carduus*) and the male plant as an *Aster*. In fruit, the female heads do resemble thistles. According to Johnston (1949: 292) the male heads are deeper orange than the female, as well as being smaller.

CANAL ZONE: Fort San Lorenzo, *Burch et al. 1040* (GH, MO). Near water reservoir W of Cocolí, *Croat 9164* (MO). Allbrook site, *Dwyer & Robyns 33* (MO). Madden Dam Area, *Ebinger 849* (GH, MO). Balboa Heights, *Greenman & Greenman 849* (MO). Madden Dam area, *Hunter & Allen 434* (MO). Curundú, *Kozlovsky & Sawyer s.n.* (MO). Madden Dam area, *Porter et al. 4005, 4053* (both MO). Balboa, Sosa Hill, *Standley 26413* (MO). Madden Dam area, *Stern et al. 48* (MO). Fort San Lorenzo, *Tyson & Blum 3669* (FSU, MO). CHIRIQUÍ: Guanabano, *Croat 22625* (MO). DARIÉN: Isla Saboga, *Duke 10362* (MO). PANAMÁ: Isla del Rey, *Duke 9537* (MO). Isla Chepillo, *Duke 10333* (MO). San José Island, *Johnston 1286, 1333, 1333A* (all GH, MO). Sabanas near Chepo, *Hunter & Allen 26* (MO). Chagres Valley around Alhajuela forests, *Pittier 2355* (GH). W of Chepo on road to Panama City, *Tyson 5375* (MO).

105. ONOSERIS

Onoseris Willd., Sp. Pl. 3: 1702. 1804. TYPE: *O. purpurea* (L.f.) Blake.

Seris Willd., Ges. Naturf. Freunde Berlin Mag. Neuesten Entdeck. Gesammten Naturk. 1: 139. 1807. TYPE: *S. onoseroides* (H.B.K.)Willd. ex Spreng.

Hipposeris Cass., Dict. Sci. Nat. 33: 464. 1824. TYPE: No valid combination made. Jackson, Index Kew. 2: 1164 (1894) makes a combination, *H. salicifolia*, but as a synonym of *Onoseris salicifolia* H.B.K.

Centroclinium D. Don, Trans. Linn. Soc. 16: 254. 1830. TYPE: *C. albicans* D. Don.

Caloseris Benth., Pl. Hartw. 88. 1841. TYPE: *C. rupestris* Benth.

Cladoseris Spach, Hist. Nat. Veg. 10: 35. 1841. TYPE: *C. annua* (Less.) Spach.

Cursonia Nutt., Trans. Amer. Philos. Soc., n.s. 7: 422. 1841. TYPE: *C. peruviana* Nutt.

Schaetzellia Klotzsch, Allg. Gartenzeitung 17: 82. 1849. TYPE: *S. deckeri* Klotzsch.

Rhodoseris Turcz., Bull. Soc. Imp. Naturalistes Moscou 24: 38, *tab. 2*. 1851. TYPE: *R. conspicua* Turcz.

Cataleuca Koch & Fintelm., Wochenschr. Gärtnerei Pflanzenk. 2: 163. 1859, nom. nud. TYPE: *C. rubicunda* Koch & Fintelm, substitute name for *Isotypus onoseroides* H.B.K.

Pereziopsis Coult., Bot. Gaz. (Crawfordsville) 20: 52, *pl. 6*. 1895. TYPE: *P. Donnell-Smithii* Coult.

Shrubs (annual herbs) with ribbed, (smooth) white or gray lanate stems. *Leaves* alternate, variable in size, usually deeply parted, slightly lanate above, densely lanate beneath, petiolate or sessile; petiole, if present, alate, lobulose, or both in most species. *Inflorescences* loosely paniculate or of solitary heads. *Heads* either discoid (in Panama) or disciform, turbinate; involucral bracts in several series, ovate to lanceolate, lanate or variously pubescent on the outer surface; receptacle flat, fimbrillate, pilose or naked; in disciform heads the outer series of florets with a strap-shaped ligule and 2 minute inner teeth, the inner series either actinomorphic, tubular, 5-dentate, or slightly zygomorphic with 1 segment larger than the other 4; in discoid heads, the florets all fertile, zygomorphic, with 1 of the 5 corolla lobes expanded, the anthers with sagittate basal appendages, acute or with spreading hairs at the tip, the style claviform or cylindrical. *Achenes*

more or less terete, ribbed, the ribs glabrous or variously pubescent; pappus of abundant yellowish setose bristles.

The genus *Onoseris* with about 24 species extends from Mexico to Argentina with a concentration of shrubby species in Central America and the extreme western Andes. The annual species are all restricted to high Andean habitats. Four species occur in Central America and 9 species are endemic to Peru. The genus, usually placed in the Gochnatinae, has species with some characters of this subtribe, e.g., actinomorphic corollas, but other species have zygomorphic corollas, characteristic of the Nassauviinae.

Literature:

Ferreyra, R. 1944. Revisión del género *Onoseris*. Jour. Arnold Arbor. 25: 349–395, 9 *pls*.

1. **Onoseris onoseroides** (H.B.K.) B. L. Robinson, Proc. Amer. Acad. Arts 49: 514. 1913.—Fig. 105.

Isotypus onoseroides H.B.K., Nov. Gen. Sp. Pl. 4: 12. *tab.* 307. 1820 (ed. 1818). TYPE: Venezuela, in hot areas near Tui River, *Humboldt & Bonpland* (not seen).
Seris onoseroides (H.B.K.) Willd. ex Spreng., Syst. Veg. 3: 426. 1820.
Onoseris paniculata DC., Prodr. 7: 33. 1838, nom. nud., cited under *Isotypus onoseroides*.
Hilairia paniculata DC., Prodr. 7: 33. 1838, nom. nud., cited under *Isotypus onoseroides*.
Caloseris rupestris Benth., Pl. Hartw. 88. 1841. TYPE: Guatemala, mountain of Chorro, *Hartweg* (not seen).
Schaetzellia deckeri Klotzsch, Allg. Gartenzeitung 17: 82. 1849. TYPE: Grown in the Decker family's private botanic garden in Berlin from seeds sent from Colombia (not seen).
Rhodoseris conspicua Turcz., Bull. Soc. Imp. Naturalistes Moscou 24: 39, *tab.* 2. 1851. TYPE: Mexico, *Jürgensen* (not seen).
Cataleuca rubicunda Koch & Fintelm., Wochenschrift Gärtnerei Pflanzenk. 2: 163. 1859, nom. nud., substitute name for *Isotypus onoseroides* H.B.K.
Onoseris isotypus Benth. & Hook., Gen. Pl. 2: 487. 1873, substitute name for *Isotypus onoseroides* H.B.K.
Seris conspicua (Turcz.) Kuntze, Rev. Gen. Pl. 1: 364. 1891.
S. rupestris (Benth.) Kuntze, Rev. Gen. Pl. 1: 364. 1891.
Onoseris rupestris (Benth.) Greenman, Proc. Amer. Acad. Arts 41: 268. 1905.
O. conspicua (Turcz.) Greenman, Proc. Amer. Acad. Arts 41: 268. 1905.

Shrubs to 4 m tall with gray, wooly stems. *Leaves* few, clustered primarily near the base of the plant, (12.5–)20(–30) cm wide, (12–)38(–38) cm long, deeply parted, almost pinnately compound, the terminal segment cordate or sagittate, the remaining segments forming paired, ovate to lanceolate, dentate lobes along the petiole, above with wispy, scattered, long, white hairs, densely gray lanate beneath. *Inflorescences* paniculate, 140–450 mm tall; pedicles bracteate, lanate. *Heads* discoid, turbinate, 9–23 mm tall; involucral bracts in 7–8 series, lanceolate, acuminate, increasing in size inwards; receptacle flat, fimbrillate, florets 4–11 per head, the corolla red, zygomorphic, 5-parted with 1 tooth larger than the other 4, glabrous, 15–25 mm long. *Achenes* columnar, truncate, ca. 6 mm long, with 4–5 narrow ribs covered with long, ascending and short, yellow trichomes; pappus of numerous, yellow, setose bristles to 17 mm in length.

Onoseris onoseroides is a striking species with red flowering heads. Its wide distribution from Guatemala to Venezuela and Colombia has led to its being

FIGURE 105. *Onoseris onoserioides* (H.B.K.) B. L. Robinson.—A. Inflorescence (× ⅓).—B. Leaf (× ⅓).—C. Corolla (× 2⅘).—D. Achene (× 2⅘). [After *Croat* 22223 (MO).]

described as a different species from several parts of its range. However, the characters such as more or less pubescence on the leaves appear to be simply geographical or even individual variation when plants from the entire range are examined.

CHIRIQUÍ: Caldera on Río Chiriquí Viejo, *Maurice* 850 (US). Roadside from Paso Canoas to Cañas Gordas 18 mi from Paso Canoas, Quebrada de Vuelta, *Croat* 22223 (MO).

106. TRIXIS[66]

Trixis P. Browne, Civ. Nat. Hist. Jam. 312, *pl. 33, fig. 1.* 1756. TYPE: *T. inula* Crantz.

Dolichlasium Lag., Amen. Nat. 1: 33. 1811. TYPE: *D. lagascae* D. Don.
Prionanthes Schrank, Pl. Rar. Hort. Acad. Monac. 2: 51. 1820. TYPE: *P. antimenorrhoea* Schrank.
Tenorea Colla, Hort. Ripul. 137. 1824. TYPE: *T. berteri* Colla, nom. illeg. = *Trixis inula* Crantz.
Platycheilus Cass., Dict. Sci. Nat. 34: 212. 1825. TYPE: *P. ochroleucus* (Cass.) Cass.
Castra Vell., Fl. Flum. 342. 1825. TYPE: *C. regia* Vell. = *Trixis antimenorrhoea* (Schrank) Mart.
Bowmannia Gardn., Icon. Pl. *tab. 519.* 1843. TYPE: *B. verbascifolia* Gardn.

Shrubs arising from horizontal, woody fissured rhizomes; stems bearing prominent persistent leaf bases, glabrous or nearly so, but young branches and inflorescences usually pubescent. *Leaves* alternate, lanceolate, several times as long as wide, the margins irregularly denticulate (rarely serrate), pubescent or rarely glabrous, usually slightly recurved or revolute, venation reticulate, the midrib and nerves usually prominent beneath, petiolate, subsessile or sessile. *Inflorescence* terminal, usually compound (corymbose or paniculate heads rarely solitary at branch tips). *Heads* appearing disciform or radiate, cylindrical; involucre uniseriate subtended by 3–7 spreading accessory bracts, the involucral bracts 7–10, linear to oblong, usually equal, convex or keeled, the margins pubescent and tightly connivent; receptacle flat, alveolate, fimbrillate; florets all perfect, usually 11–15 or 17–25, the inner florets similar to the outer ones but usually smaller, the corollas yellow becoming whitish, bilabiate, the outer lip elliptical or oblong, usually spreading in the outer flowers, always revolute in the inner flowers, apically 3-toothed, the inner lip 2-parted, the anthers with oblong tips, basally auriculate, the style branches flattened, truncate and with a crown of sweeping hairs at the apex. *Achenes* fusiform with a short beak or an apical constriction, 5-ribbed, covered with colorless double hairs that release mucilage when wetted (except in *T. inula*) and with small glands; pappus of numerous, tawny or white, setose bristles in 3 or 4 series.

Literature:

Anderson, C. 1972. A monograph of the Mexican and Central American species of *Trixis* (Compositae). Mem. New York Bot. Gard. 22: 1–68.

Cabrera, A. L. 1936. Las especies, argentinas y uruguayas del género *Trixis*. Revista Mus. La Plata, Secc. Bot. 1: 31–86.

1. **Trixis inula** Crantz, Inst. Rei. Herb. 1: 329. 1766. TYPE: Jamaica, *Browne*, Herb. Linn. 1003.3, "*Perdicium radiale*" (LINN, not seen, US, microfiche).—FIG. 106.

Inula trixis L., Amoen. Acad. 5: 406. 1759. TYPE: Jamaica, *Browne*, Herb. Linn. 1003.3, "*Perdicium radiale*" (LINN, not seen, US, microfiche).

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[66] Parts of this treatment were adapted from the treatment for *Trixis* prepared by Dr. Christiane Anderson for North American Flora (in press).

Perdicium radiale L., Sp. Pl., ed. 2. 1248. 1763. TYPE: Jamaica, *Browne*, Herb. Linn. 1003.3, "*Perdicium radiale*" (LINN, not seen, US, microfiche).
Solidago fruticosa Miller, Gard, Dict., ed. 8. *Solidago* no. 31. 1768. TYPE: Mexico, Veracruz, *Houston* (BM, holotype, not seen).
Perdicium laevigatum Bergius, Kongl. Vetensk. Acad. Handl. 33: 238, *pl.* 7. 1772. TYPE: Panama, Portobelo, *Pihl* (SBT, holotype, not seen).
P. havanense H.B.K., Nov. Gen. Sp. Pl. 4: 155. 1820 (1818). TYPE: Cuba, Havana, *Humboldt & Bonpland* (P, holotype, not seen).
Trixis berteri Colla, Hort. Ripul. 137. 1824. TYPE: Colombia, Santa Marta, *Bertero* (TO, holotype, not seen).
T. fructescens P. Browne ex Spreng., Syst. Veg. 3: 501. 1826. TYPE: Jamaica, *Browne*, Herb. Linn. 1003.3, "*Perdicium radiale*" (LINN, not seen, US, microfiche).
T. laevigata (Bergius) Lag. ex Spreng., Syst. Veg. 3: 501. 1826.
T. havanense (H.B.K.) Spreng., Syst. Veg. 3: 501. 1826.
T. corymbosa D. Don, Trans. Linn. Soc. London 16: 188. 1830. TYPE: "in Mexico," *Sessé & Mociño* (G, holotype, not seen).
T. glabra D. Don, Trans. Linn. Soc. London 16: 297. 1830. TYPE: Mexico, Veracruz, prope Laguna Verde, *Schiede & Deppe* (location of type unknown).
T. frutescens var. *obtusifolia* Less., Linnaea 6: 411. 1831. TYPE: Mexico, Veracruz, prope Laguna Verde, *Schiede & Deppe* (location of type unknown).
T. frutescens var. *glabrata* Less., Syn. Gen. Comp. 414. 1832. TYPE: Panama, Portobelo, *Pihl* (SBT, holotype, not seen).
T. frutescens β *angustifolia* DC. in DC., Prodr. 7: 69. 1838. LECTOTYPE: Cuba, Havana, *de la Varga* (G-DC, not seen).
T. ehrenbergii Kunze, Linnaea 16: 317. 1842. TYPE: Grown from seed sent by Ehrenberg from Mexico (LZ, destroyed).
T. radialis (L.) Kuntze, Rev. Gen. Pl. 1: 370. 1891.
T. radialis α *pubescens* Kuntze, Rev. Gen. Pl. 1: 370. 1891. TYPE: Venezuela, La Guayra—Caracas, *Kuntze 1409* (NY, holotype, not seen).
T. radialis β *subglabrata* Kuntze, Rev. Gen. Pl. 1: 370. 1891. TYPE: unknown.
T. deamii B. L. Robinson, Proc. Amer. Acad. Arts 45: 411. 1910. TYPE: Guatemala, Zacapa, *Deam 6359* (GH, holotype; MICH, US, isotypes).
T. adenolepis Blake, Contr. U.S. Natl. Herb. 22: 654. 1924. TYPE: Guatemala, Gualan, *Deam 324* (US, holotype; GH, isotype).
T. chiantlensis Blake, Brittonia 2: 359. 1937. TYPE: Guatemala, Chiantla, Huehuetenango, *Skutch 1957* (GH, holotype, US, photo and fragment of holotype).

Perennial *herbs* 0.5–3 m tall, erect, much branched with glandular trichomes on the vegetative parts. *Leaves* petiolate; blades 24–70(–165) mm long, 5–22 mm wide, linear-lanceolate to elliptical, acute, attenuate or slightly truncate at the base, glabrate above with scattered glands and hairs, beneath strigose to pilose, rarely villous and sparsely glandular; petioles 1–7 mm long. *Inflorescences* paniculate or corymbose; peduncles sparsely glandular, strigose to pilose or glabrous, rarely sericeous. *Heads* hermaphrodite; involucral bracts 7–9, 8–13(–15) mm long, linear or oblong, acute, convex, sparsely glandular, sparsely strigose to strigose, rarely glabrous; receptacle fimbrillate; florets 8–15 per head, the outer florets 5–9 mm long, the corolla yellow. *Achenes* (4–)5(–9) mm long, beaked, covered with double hairs that are usually not mucilage-releasing, and glandular trichomes, the beak about ¼ the length; pappus, 7–11 mm long, of setose tawny bristles. Chromosome number $2n = 54$ (Federov, 1969).

Trixis inula is common in sandy open areas, along roadsides, and in thickets of secondary growth, generally in lowland regions of deciduous forest. It occurs from the southeastern tip of Texas south throughout Central America, east to northern Colombia and Venezuela, and in the West Indies.

FIGURE 106. *Trixis inula* Crantz.—A. Habit (× ½).—B. Floret (× 2⅘).—C. Achene (× 2⅘). [After *Croat 21892* (MO).]

CHIRIQUÍ: 8 km W from Puerto Armuelles, 150 m, *Busey 444* (MO). 1 mi W of airport at Puerto Armuelles, sea level, *Croat 21892* (MO). DARIÉN: Second large point just before Punto Alegre, NE of Garachine, *Gentry 4054* (MO). HERRERA: Vic. of Las Minas along Río Las Trancas, *Stern et al. 1785* (MO). LOS SANTOS: Tonosí, Guánico, 117 ft, *Stern et al. 1843* (MO). Road from Tonosí to Guánico (at Río Guánico), *Tyson et al. 3113* (MO). PANAMÁ: Sea Beach from Panamá Vieja to Bella Vista, *Allen 823* (MO). Cerro Campana, 850 m, *Busey 858* (MO); *Dwyer et al. 4852* (MO). VERAGUAS: Cordillera Central, headwaters of Río Cañazas, 300–600 m, *Allen 201* (MO).

XIII. LACTUCEAE

W. G. D'Arcy[67] and A. Spencer Tomb[68]

Lactuceae Cass., Jour. Phys. 88: 151. 1819. type: *Lactuca* L.

Chichorieae Dumort., Anal. Fam. Pl. 30. 1829. type: *Cichorium* L.

Herbs or rarely *trees* or *shrubs*; pubescence various; sap mostly milky. *Leaves* alternate or in a basal rosette, mostly dentate, often variously incised or dissected, the bases often clasping. *Inflorescences* various. *Heads* ligulate, rarely almost discoid; involucral bracts herbaceous or nearly hyaline, often basally thickened in fruit, in 1–several, unequal, mostly graded series, the innermost series sometimes subequal and valvate or basally connate; receptacle mostly flat or slightly convex, naked or paleaceous; paleas hyaline; florets all ligulate, all perfect, all fertile, the outer series often with larger corollas or differentiated fruits, the corollas bilaterally symmetric, a slender and flat, 5-dentate ligule (limb) mostly exserted from the involucre, glabrous or pubescent, the anthers 5, appendaged, basally sagittate or auriculate, the style branches slender, papillose or puberulent, apically narrowed, obtuse or truncate, ventrally stigmatic for the whole length, the shaft often apically pubescent, the ovary terete or compressed, sometimes with an apical nectary surrounding the style base. *Fruit* an achene, smooth, rugose or tuberculate, sometimes ribbed or sulcate, apically truncate or beaked, sometimes compressed; carpopodium mostly inconspicuous; pappus mostly of numerous fine, strigose bristles but sometimes of hairs, stout bristles, or plumose bristles, rarely of scales or wanting.

This is the most distinct of the tribes of Compositae, readily separated by the all-ligulate corollas, all-perfect florets, and milky sap. While usually homogamous, the florets should not be interpreted as all alike, for the outer corollas are frequently longer, broader, and of slightly different color than the inner corollas, and the outer achenes are also sometimes of different color, texture, or shape.

The tribe is best represented in temperate regions of the northern hemisphere. The genera occurring in Panama are best developed in temperate regions. Only *Hieracium* includes species native to the New World. With the exception of *Cichorium*, which may be cultivated in Panama, all Panamanian members of this tribe have yellow flowers.

In addition to the species treated here, *Launaea intybus* (Jacq.) Beauv. is to be expected. It is a pan-tropical weed of lowlands often occurring in areas with dry periods. It has yellow corollas, coarsely toothed, pandurate leaves and dimorphic achenes, the outermost compressed and the inner series terete, the pappus of numerous fine hairs and strigulose bristles. In upland Chiriquí, *Lactuca sativa* L. (lettuce, lechuga) is a year-round crop plant, but only one collection, *Mori & Bolten 7250* (MO) from 5 km NW of Cerro Punta at Las Nubes, is known.

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Lowland Panama is not suitable for cultivation of traditional strains of *Lactuca sativa* but recently developed strains may be satisfactory and are perhaps grown for salads. *Lactuca* may be recognized by its flattened and beakless achenes (achenes of *Sonchus* are flattened but lack beaks), and pappus of strigose bristles. In upland regions, endive, *Cichorium endiva* L., and chicory, *C. intybus* L., are probably grown from time to time. *Cichorium* may be recognized by its pappus of small scales and its sky-blue corollas.

a. Achenes with long beaks.
  b. Pappus bristles plumose, at least in part; receptacle paleaceous; involucral bracts overlapping in several similar graded series ..... 108. *Hypochoeris*
  bb. Pappus bristles not plumose; receptacle naked; involucral bracts dimorphic, composed of several, short outer series and a long, valvate inner series .... 110. *Taraxacum*
aa. Achenes all unbeaked.
  c. Leaves entire or dentate but not incised; achenes columnar or wanting; stems and leaves with long, tawny hairs (over 2.5 mm long) ..... 107. *Hieracium*
  cc. Leaves mostly incised or dissected; achenes much compressed; plants without long tawny hairs (sometimes with gland-tipped bristles).
    d. Heads less than 6 mm tall; involucral bracts few in 2 unlike series, each equal, only slightly overlapping; leaves mostly basal in a rosette ..... 111. *Youngia*
    dd. Heads more than 6 mm tall; involucral bracts numerous in several graded, overlapping series; leaves mostly cauline ..... 109. *Sonchus*

107. HIERACIUM

Hieracium L., Sp. Pl. 799. 1753; Gen. Pl., ed. 5. 350. 1754. TYPE: *H. murorum* L.

Perennial *herbs*; stems mostly with long hairs, often also with short hairs, dendritic hairs, glandular hairs, or bristles; sap milky. *Leaves* often in a basal rosette, cauline leaves present or not, obovate or oblanceolate, entire, dentate or undulate, petiolate or not, sometimes clasping the stem. *Inflorescence* scapose, paniculate, or rarely of a solitary sessile head; peduncles or pedicels often pubescent, sometimes subtended by narrow bracts. *Heads* ligulate; involucral bracts in 2–several, graded, imbricate series, the innermost often subequal, nearly valvate; receptacle flat or slightly convex, naked; florets all perfect, all fertile, the corollas yellow (Panama), white, orange or purplish, the ligule short or long, 5-dentate, the tube sometimes apically pubescent, the anthers appendaged, with sagittate or auriculate bases, the style branches slender, papillose, sometimes dark. *Achene* cylindrical or fusiform, often prominently ribbed or sulcate; pappus of numerous, mostly tawny bristles in 1 series. *Pollen* echinolophate, usually 3-colporate. Base chromosome number $x = 9$.

Hieracium comprises more than 1000 apomictic "species" in Europe and perhaps a dozen sexual species in the New World north of Colombia.

In Panama, species of *Hieracium* may be recognized by their stout, long, tawny hairs and their inconspicuous, ligulate corollas. "Hawkweed," "Hierba del Gavilán."

Literature:

Robinson, B. L. & J. M. Greenman. 1904. Revision of the Mexican and Central American species of *Hieracium*. Proc. Amer. Acad. Arts 40: 14–24.

Zahn, K. H. 1923. Compositae-*Hieraceum*. *In* A. Engler (editor), Das Pflanzenreich IV. 280 (Heft. 79): 1100–1108, 1115–1124.

a. Leaves narrow, mostly less than 2 cm wide, more than 7 times as long as wide, the minute teeth conspicuous; achenes columnar to the apex; upland plants.
  b. Involucral bracts puberulent with small, whitish, eglandular hairs, a few dark, glandular hairs sometimes present, the margins mostly herbaceous; inflorescence much-branched, many-headed; leaves cauline and basal ..... 1. *H. absissum*
  bb. Involucral bracts with copious long, black, often glandular hairs, the margin hyaline at both sides and tips; inflorescence crowded, little-branched, few-headed; leaves mostly basal ..... 3. *H. irasuense*
aa. Leaves spatulate, often more than 2 cm wide, mostly less than 7 times as long as wide, the teeth, if present, inconspicuous; achenes tapering in the upper half; lowland plants ..... 2. *H. gronovii*

1. **Hieracium absissum** Less., Linnaea 5: 132. 1830. TYPE: Mexico, *Schiede & Deppe 190* (MO).—FIG. 107A–C.

Slender, erect *herb* to 60 cm tall; stems hirsute with stout, strigose hairs to 8(–10) mm long, more so near the base; rootstock of stout fibers, short; sap milky. *Leaves* narrow, oblong or lanceolate, subentire, with widely separated minute, ?glandular teeth, to 11 cm long, ca. 1 cm wide, smaller upwards, sometimes discolorous, both sides sparingly pilose, apically acute, basally narrowed but not forming a distinct petiole, the base slightly clasping. *Inflorescence* a many-headed panicle, the branching not truly dichotomous; peduncle glabrate below; pedicels slender, 5–10 mm long with gland-tipped short bristles and short, weak, dendritic hairs, subtended by elongate, linear bracts, and sometimes with minute scales along the length. *Heads* small, 7–8 mm long, ligulate; involucre cylindrical, narrow, spreading in fruit, of ca. 15 inner, subequal, basally imbricate, narrow bracts with margins hyaline only sometimes in the lower half, and several, smaller, graded outer bracts; florets numerous, all ligulate, all perfect, all fertile, the corollas yellow, ca. 6 mm long, with a few long hairs near the apex of the tube, exserted ca. 3 mm from the involucre, the ligule broad, with 5 rounded, short teeth, the anthers ca. 1.5 mm long, the appendages prominent, the bases sagittate, the style apically puberulent, the branches slender, dark, puberulent. *Achene* black, cylindrical, prominently many-ribbed, 2 mm long; pappus of numerous, tawny strigose bristles in 1 series, persistent.

The species may be recognized by its inflorescence of numerous small heads and linear, often pilose stems. A few long black hairs may be present on the involucral bracts, as in *H. irasuense*, but this pubescence is not dominant. It ranges from Mexico to Panama, where it occurs in upland Chiriquí.

CHIRIQUÍ: Volcán de Chiriquí, Boquete District, 7000 ft, *Davidson 871* (MO). 6.7 mi W of Boquete, 8000 ft, *Luteyn 1481, 1507* (both MO). 3 mi N of El Volcán, 5000 ft, *Tyson 5837* (MO).

2. **Hieracium gronovii** L., Sp. Pl. 802. 1753. TYPE: America, *Kalm*, Herb. Linn. 954.16 (LINN, not seen, MO, microfiche).

H. panamense Blake, Contr. U.S. Natl. Herb. 22: 658. 1924. TYPE: Panama, *Busch 1* (US).

Perennial, scapose *herbs*; stems glabrate above with dense or sparse long hairs on the lower portion; roots coarsely fibrous with a short, ill-defined caudex.

FIGURE 107. *Hieracium*.—A–C. *H. absissum* Less.—A. Base of plant (× ⅖).—B. Inflorescence (× ⅖).—C. Involucral bract (× 5). [After *Tyson* 5837 (MO).]—D. *H. irasuense* Benth. Involucral bract (× 5). [After *Allen 4770* (MO).]

Leaves basal, forming a (sometimes ephemeral) rosette and cauline, spatulate, to 15 cm long, apically rounded or obtuse, basally cuneate, sessile, the midvein prominent with ca. 4 lateral veins on each side, conspicuously hirsute-pilose with abundant, scattered tawny or reddish hairs 3–5 mm long, the cauline leaves sometimes in alternate fascicles, mostly smaller. *Inflorescence* an open, scapose panicle to 60 cm tall; peduncle and pedicels with scattered stalked glands and tomentulose with fine simple hairs; pedicels 5–10 mm long with minute bractlets at the base or along the length. *Heads* ligulate, ca. 10 mm long; involucre sometimes drying dark, of numerous linear bracts in an inner, subequal series and 1 or 2 short, outer series, dorsally pilose with simple hairs and sometimes with gland-tipped bristles, the broad margins glabrate; receptacle naked; florets all ligulate, all perfect, all fertile, the corollas yellow, slightly exceeding the involucre, the ligule with short, rounded, sometimes fimbriate teeth. *Achene* nearly black, 3–4 mm long, linear, prominently many-striate, puberulent; pappus of numerous strigose, tawny bristles.

This species may be recognized by its wide leaves, narrow achenes, and fimbriate corolla lobes. It is a native of the eastern United States but has been collected in Honduras as well as in Panama.

PANAMÁ: Near Alhajuela, *Busch 1* (US).

3. **Hieracium irasuense** Benth. in Örst., Vidensk. Meddel. Dansk Naturhist. Foren. Kjøbenhavn 1851: 113. 1853. TYPE: not seen.—FIG. 107D.

Hieracium maxonii Blake, Contr. U.S. Natl. Herb. 22: 660. 1924. TYPE: Panama, *Maxon 5351* (US).

Perennial *herbs*; roots numerous, coarse; sap milky; stems with scattered or dense, long, stout, tawny hairs. *Leaves* mostly basal, oblanceolate or obovate, to 10 cm long, subentire or undulate, mostly denticulate with minute glandular teeth, apically acute or obtuse, basally cuneate, sometimes broadly so and clasping, sometimes narrowed into a distinct petiolar region, midvein prominent, the pinnate venation often irregular, the cauline leaves often smaller, narrower, acute. *Inflorescence* scapose, several-headed, elongate (to 40 cm tall) sparingly branched, linear bracts sometimes subtending the branches, the upper portion tomentose with gland-tipped bristles and whitish, simple or sparingly dendritic hairs. *Heads* 8–10 mm long, ligulate; involucre drying dark, of numerous linear bracts in an inner, subequal series and several, similar, graded outer bracts, dorsally pilose with dark glandular hairs, the margins sometimes conspicuously lighter; receptacle naked; florets all ligulate, all perfect, all fertile, the corollas yellow, slightly exceeding the involucre, the ligule with short rounded teeth, the anthers with conspicuous appendages, basally sagittate, the style branches slender, puberulent. *Achene* nearly black, 3 mm long, cylindrical, prominently many-striate; pappus of numerous, strigose, tawny bristles.

This species resembles *H. absissum*, but apparent differences are in the pubescence of the involucral bracts, in the more elaborate inflorescence with

larger heads, and in the more pubescent pedicels. Both species are known in Panama mainly from upland Chiriquí.

CHIRIQUÍ: Forested ridges S of Finca Lérida, 6000–7000 ft, *Allen 4770* (MO). Potrero Muleto to summit, Volcán de Chiriquí, 3500–4000 m, *Woodson & Schery 395* (MO). Near Casita Alta, Volcán de Chiriquí, 1500–2000 m, *Woodson et al. 818* (MO). Loma Larga to summit, Volcán de Chiriquí, 2500–3380 m, *Woodson et al. 1086* (MO). Summit of Chiriquí Volcano, 3374 m, *Maxon 5351* (US).

108. HYPOCHOERIS

Hypochoeris L., Sp. Pl. 810. 1753; Gen. Pl., ed. 5. 352. 1754. TYPE: *H. glabra* L.

Hypochaeris auct., non L., Gen. Pl., ed. 5. 352. 1754.

Annual or perennial *herbs*, often scapose rosette plants; roots fibrous or stout; sap milky. *Leaves* alternate, often in a basal rosette, mostly oblanceolate, entire or variously dentate to pinnatisect, glabrate to pubescent, the hairs sometimes stout. *Inflorescence* a simple or branched, leafless scape, or an open panicle; small bracts sometimes present. *Heads* sometimes large, the florets all ligulate, all perfect, all fertile, but sometimes dimorphic; involucre cylindrical to campanulate, enlarging in fruit, the bracts numerous in several graded, imbricate series, sometimes apically differentiated; receptacle flat or convex; paleas hyaline, partly enfolding the ovaries, apically slender, about as long as the outer ligules; corollas yellow, orange or white, glabrate or pubescent at the base of the throat, the outer series exceeding the involucre, broad, apically narrowed, with 5 prominent narrow teeth, inner series narrow, mostly not exceeding the involucre, stamens 5, the anthers appendaged, the style ascending-pubescent, basally glandular, the style branches slender. *Achenes* of peripheral florets truncate in some species, those of the inner florets long-beaked, sulcate, tuberculate-hispid; pappus of numerous bristles, in one or more similar or dissimilar series, in some species differentiated into stout or slender, strigose or plumose, or short or long series. *Pollen* echinolophate. Base chromosome numbers $x = 4, 5, 6, 7$.

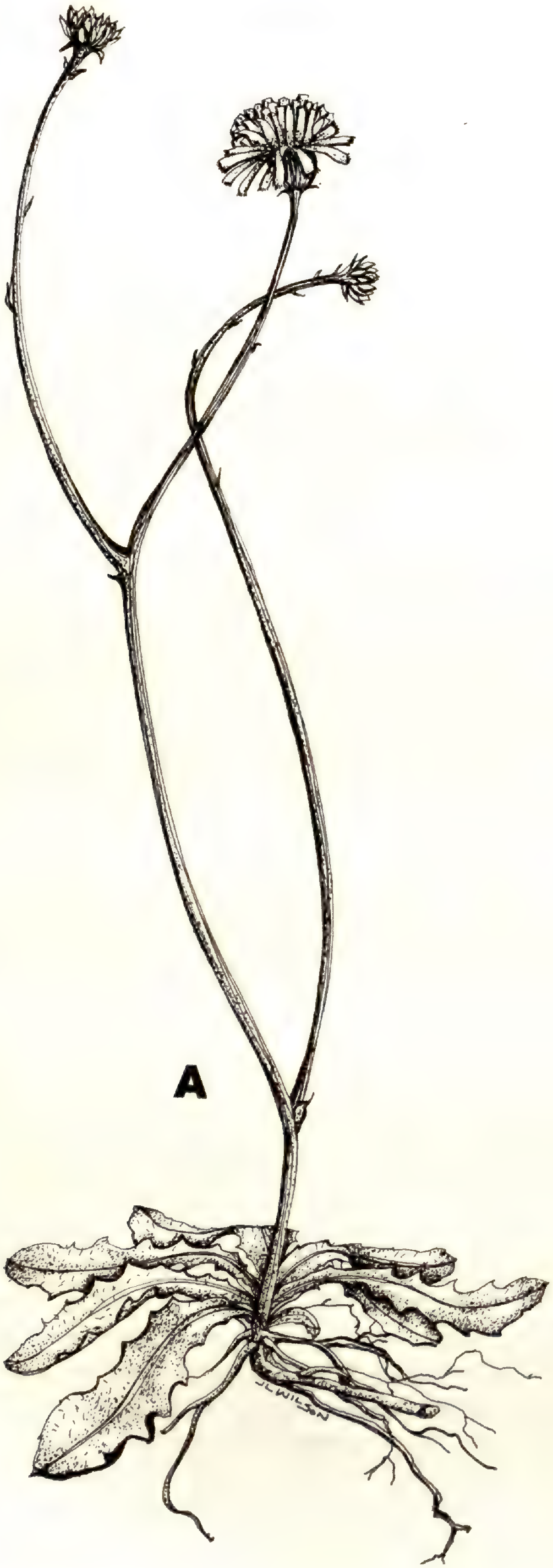
Hypochoeris is best represented in temperate South America and Europe. The species treated here is widespread. It is a member of subgenus *Hypochoeris*, characterized by a pappus differentiated in 2 unlike series, the innermost plumose and the outer series shorter and strigose.

Literature:

Hegi, G. 1954. Illustrierte Flora von Mittel-Europa. 6(2): 1008–1016, *fig. 274.*

1. **Hypochoeris radicata** L., Sp. Pl. 811. 1753. TYPE: not seen.—FIG. 108.

Perennial rosette *herbs*; stems scapose, sometimes branched to 60 cm tall; rootstock sturdy, sometimes branched; sap milky. *Leaves* mostly basal, numerous, sessile, to 8 cm long, oblanceolate, crenate to lacerate, the sinuses mostly rounded, pilose-hispid above and beneath with stout, unicellular hairs, the midvein prominent, the lateral veins obscure, leaves of the scape mostly reduced to scales or wanting. *Inflorescences* of 1–several, branched, scapose peduncles to 25 cm tall, pilose, peduncles green, glabrate upwards; scalelike bracts often present.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Heads showy, yellow, ligulate; involucre ca. 10 mm high, the bracts numerous in several graded series, acute with slightly differentiated, reddish, ciliate tips, glabrous but the midvein often with bristles; receptacle convex, ca. 3 mm across; paleas hyaline with a prominent, double costa, basally half-enfolding the achene, apically slender, exceeding the ligules; florets numerous, all ligulate, perfect and fertile, the corollas dimorphic, the outer series ca. 15 mm long, the ligule ca. 4 mm wide, apically narrowed with 5 acute, prominent, red-tipped teeth, glabrous, drying green, the inner series shorter, narrower, yellow, the anthers yellow, the style apically ascending-pilose, the style branches linear, yellow. *Achene* dark, sulcate, tuberculate, long-beaked; pappus of numerous bristles in several series, the innermost plumose, the outermost strigose.

This species is perhaps of European origin but now occurs widely in temperate and cool tropical regions. It is distinct from related genera in the conspicuous paleas of the heads. In Panama, *Hypochoeris radicata* is known only from one fragmentary collection, hence the present description is incomplete in some details. "Cat's Ears," "Hierba de Halcón."

CHIRIQUÍ: Valley of the upper Río Chiriquí Viejo, *White & White* 92 (MO).

109. SONCHUS

Sonchus L., Sp. Pl. 793. 1753; Gen. Pl., ed. 5. 347. 1754. TYPE: *S. oleraceus* L.

Robust *herbs* (Panama) or trees; stems, often hollow, glabrous or pubescent, often with gland-tipped bristles; rootstock fibrous or stout, sometimes divided, sometimes creeping; sap milky, bitter. *Leaves* alternate, in a basal rosette or cauline, dentate to dissected, often incised, the teeth with callose or spinose tips, often glabrous, basally auriculate or not. *Inflorescence* mostly paniculate, sometimes scapose but not solitary; peduncles glabrous to pilose, sometimes with gland-tipped bristles; pedicels often subtended by foliaceous bracts. *Heads* ligulate, mostly about as broad as long, slightly broader after anthesis; involucre of numerous similar bracts in several graded series, imbricate or the innermost series sometimes valvate, narrow and acute, often basally swollen in fruit; receptacle flat or convex, mamillose, naked; florets numerous, all ligulate, all perfect, all fertile, the corolla yellow, rarely white, with 5 acute teeth, the tube apically pilose, the outer series sometimes pinkish dorsally, exceeding the involucre, the inner series smaller, the anthers 5, connate, with deltoid appendages, basally sagittate, the style apically pubescent, the branches narrow, puberulent, sometimes dark. *Achenes* mostly alike but sometimes the outermost series lighter and differing in texture, cylindrical or compressed, sometimes flat, oblong, ellipsoidal or lachrymiform, beakless, sulcate or ribbed, rugose or smooth; pappus of strigulose, silky, white bristles or of numerous, persistent, capillary hairs and fewer, stouter, deciduous bristles. *Pollen* echinolophate, mostly 3-colporate, with a tendency to extra lacunae at the poles. Base chromosome numbers $x = 7, 8, 9$.

←

FIGURE 108. *Hypochoeris radicata* L.—A. Habit (× ½).—B. Achene (× 5). [After *White* 92 (MO).]

Sonchus is an Old World genus of about 50 species centered in Europe and Africa. About 4 species are now widespread and 2 of these are naturalized in Panama. Robust, yellow-headed weeds with stout rootstocks, they may become troublesome weeds. Not known to be toxic, they are unpalatable to cattle and have reputed medicinal value in some countries. "Sow thistles," "Cerraja."

Literature:

Boulos, L. 1960. The genus *Sonchus*, a general systematic treatment. Bot. Not. 113: 400–420.

a. Leaves incised, the apical segment truncate, the auricles clasping the stem pointed, the margins not decidedly prickly to the touch; achene compressed but not flat, rugose with ribs on the sides ---------- 2. *S. oleraceus*

aa. Leaves dentate, if incised then lacking a conspicuous apical segment, the auricles clasping the stem rounded (dentate), the margins prickly; achene flat, smooth, with narrow sulci on the sides ---------- 1. *S. asper*

1. **Sonchus asper** (L.) Hill, Herb. Brit. 1: 47. 1769.

Sonchus oleraceus var. *asper* L., Sp. Pl. 792. 1753. TYPE: not seen.

Robust, short-lived perennial *herb* to 1 m tall; stems hollow; rootstock fibrous or stout, sometimes divided; sap milky. *Leaves* alternate, cauline, obovate, oblanceolate or spatulate, copiously spinulose-dentate, sometimes divided, apically acute, the basal portion often narrowed into a broadly winged, mostly dentate region, the basal auricles rounded and clasping the stem, glabrous, often bluish or slightly glaucous. *Inflorescence* an open, many-headed panicle; peduncle elongate or much abbreviated (Panama), sometimes with gland-tipped bristles; pedicels glabrous or with gland-tipped bristles, to 10 mm long; bracts leaflike but small. *Heads* 15–25 mm across, ligulate; involucre ca. 15 mm tall, the bracts lanceolate, in several similar, graded, overlapping series, glabrate or apically ciliolate, sometimes with a few subsessile glands; receptacle flat or convex, mamillose, naked; florets all ligulate, all perfect, all fertile, the corollas yellow, those of the outer series exceeding the involucral bracts, often reddish or grayish beneath, with 5 conspicuous obtuse teeth, the tube apically pilose, those of the inner series mostly shorter than the involucre, smaller, yellow with rounded teeth, the anthers with yellow or black appendages, basally sagittate, the style branches dark, narrow, dorsally puberulent, the shaft apically ascending-hispid, the ovary turning bright yellow or orange, the apical nectary cylindrical. *Achene* flat, lachrymiform, smooth or basally rugulose, each side with 2–4 distinct, low ridges ca. 3 mm long, reddish brown or sometimes a few tan colored; pappus strigulose, silky white, of numerous capillary hairs and fewer persistent bristles.

This species is known in Panama only in the Chiriquí uplands. Native of Europe, it is a widespread weed of temperate regions, and is established in some tropical areas. Similar to *S. oleraceus*, it grows in similar habitats. The leaves are usually less divided and more conspicuously dentate with longer, spinose mucros. "Prickly sow thistle," "Cerraja."

CHIRIQUÍ: Above Cerro Punta on slope of Cerro Respinga, 8000 ft, *D'Arcy & D'Arcy 6527* (MO). Bajo Mona, mouth of Quebrada Chiquero along Río Caldera, 1500–2000 m, *Woodson et al. 1001* (MO).

2. **Sonchus oleraceus** L., Sp. Pl. 794. 1753. TYPE: not seen.—FIG. 109.

Robust, short-lived *herb* to 1(?–1.5) m tall; stems terete, striate, hollow; rootstock stout, sometimes branched; sap milky. *Leaves* mostly cauline, obovate to oblanceolate, to 30 cm long, mostly incised, denticulate, the apical segment truncate to hastate, apically obtuse or rounded, the basal portion often narrowed into a distinct, winged, mostly entire-margined petiole, expanded into denticulate, pointed auricles clasping the stem, the teeth callose-mucronate, glabrous. *Inflorescence* an open panicle; peduncles with gland-tipped bristles; pedicels bracteate, mostly 1–3 cm long, glabrous. *Heads* showy, ligulate; involucre 10–20 mm tall, the bracts numerous in several, graded, imbricate series, narrow, herbaceous, glabrate or with a few bristles; florets all ligulate, all perfect, all fertile, the corollas yellow, the outermost series slightly exceeding the involucral bracts, yellow but sometimes dorsally reddish, the inner series slightly smaller, yellow, pilose at the base of the limb, glabrate above and below, apically mostly 5-denticulate, the anthers with yellow or darkened appendages, basally sagittate, the style apically ascending-pubescent, the branches narrow, puberulent. *Achenes* compressed lachrymiform, rugose with 2 fine sulci on each side, russet, the outermost achenes sometimes slightly thicker and lighter colored, beak wanting; pappus of numerous silky, persistent hairs and fewer, stouter, strigulose, deciduous bristles.

A native of temperate regions of the Old World, *Sonchus oleraceus* is widely distributed as a ruderal weed in temperate and cool tropical regions. It closely resembles *S. asper*, but in Panama it is the more common species. "Sow thistle," "Cerraja."

CHIRIQUÍ: Finca Collins, Boquete vicinity, *Dwyer 1966* (MO). Trail N of Cerro Punta, *Croat 10488* (MO). 2 mi N of El Hato del Volcán, *Croat 10639* (MO). Near Methodist Camp near Nueva Suisa, *Croat 13531* (MO). Between Boquete and Monte Rey, *Croat & Porter 15645* (MO). Near Las Nubes, 2.7 mi NW of Río Chiriquí Viejo W of Cerro Punta, 2200 m, *Croat 22422* (both MO). Across river from town of Cerro Punta, 6000 ft, *D'Arcy & D'Arcy 6526, 6530, 6531* (all MO). Río Chiriquí Viejo N of Volcán City, 5200–5600 ft, *Duke 9006* (MO). Boquete, Finca Collins, 5000 ft, *Dwyer & Hayden 7684A* (MO); *Ebinger 703* (MO). From Boquete to 3 mi N, 3300–4200 ft, *Lewis et al. 628* (MO). Quebrada Velo, 1800 m, *Woodson & Schery 278* (MO). COCLÉ: Hills NE of El Valle de Antón, 2000 ft, *Lewis et al. 1793* (MO).

110. TARAXACUM

Taraxacum[69] Wiggers, Prim. Fl. Hols. 56. 1780. TYPE: *T. officinale* Wiggers, typ. cons.

Small, perennial *herbs*; rootstock sometimes sturdy; sap milky. *Leaves* alternate, often in a basal rosette, variously incised or rarely entire, glabrous or pubescent, sometimes basally narrowed into a petiole. *Inflorescence* one or several scapes; peduncle hollow, terete; mostly ebracteate. *Heads* ligulate; involucre of dimorphic bracts, the outermost in 2–3 spiral, calyculate series, short, free, applied, porrect or reflexed, the innermost in 2 series, subequal, linear, valvate and basally connate or slightly imbricate, glabrous or ciliolate; receptacle naked, flat, areolate;

[69] For a list of synonyms, see Hendel-Mazzetti (1907). Only the name *Taraxacum* has been used for Panamanian material.

B

A

florets all perfect and fertile but sometimes dimorphic, the corollas yellow, white, orange, purplish or red, those of the outer florets larger, often grayish or brown, the anthers with appendages basally connate and basally sagittate, the style apically pubescent, the branches pubescent, a large nectary sometimes present, the ovaries of the outer and inner florets sometimes differing in size and ornamentation. *Achenes* all alike, oblong, sulcate, apically tuberculate, the beak elongate, basally thickened and sometimes sulcate; pappus of numerous, strigose bristles in many similar series. *Pollen* echinolophate, 3–4-colpate, often irregularly shaped. Base chromosome number $x = 8$.

Much of the genus *Taraxacum* is apomictic and comprises many local and morphologically similar elements which have been recognized as species. Depending on the circumscription of these segregates, the genus includes from 23 to over 1000 species, centered mainly in Europe and the Mediterranean basin. Several species are naturalized in North America, and the species found in Panama is almost worldwide in distribution.

Literature:

Hendel-Mazzetti, H. von. 1907. Monographie der Gattung *Taraxacum*. Leipzig.
———. 1923. Nachträge zur Monographie der Gattung *Taraxacum*. Oesterr. Bot. Zeitschr. 72: 254–275.

1. **Taraxacum officinale** Weber ex Wiggers, Prim. Fl. Holst. 56. 1780, based on *Leontodon taraxacum* L.

Leontodon taraxacum L., Sp. Pl. 798. 1753. TYPE: not seen.
L. vulgare Lam., Fl. Françoise 2: 113. 1778, renaming of *L. taraxacum* L.
Taraxacum vulgare (Lam.) Schrank, Baiersche Reise 11. 1786.
T. dens-leonis Desf., Fl. Atlant. 2: 228. 1799.

Herbs with a stout rootstock and milky sap. *Leaves* mostly basal, alternate, oblong, to 15(–25) cm long, lacerate, the lobes and teeth acute, often reflexed, narrowed into a distinct, flattened petiole, glabrate, the midvein prominent and the lateral veins weak; petiole slightly winged at the base, sometimes ciliate. *Inflorescence* scapose; peduncle terete, hollow, 1–20 cm long, yellowish or reddish, or sparingly pilose with arachnoid hairs, ebracteate. *Heads* showy yellow, ligulate, 3(–4) cm across; involucre of numerous, dimorphic bracts, the outermost in ca. 3 series, short, acute, recurving, free, sometimes reddish-tipped, the innermost in ca. 1 series, linear-acute, ciliolate, 10–15 mm long, slightly overlapping and valvate, connate in the basal half, glabrate, the tips often reddish, deflexed in fruit; receptacle naked, white, 5–10 mm across, alveolate, the persistent carpopodia sometimes conspicuous; florets numerous, 15–20 mm long, all fertile, dimorphic, the outermost 1–3 series with corollas much exceeding the involucral bracts, the ligule linear, 5-denticulate, dorsally brown with yellow margins, ventrally yellow,

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FIGURE 109. *Sonchus oleraceus* L.—A. Habit (× ⅘).—B. Achene (× 3⅓). [After *Croat* 22422 (MO).]

the base of the tube and apex of the limb sparingly pilose outside, the stamens brownish yellow, the appendages dark, acute, basally connate, basally sagittate, the filaments glabrous, the ovary tuberculate, the beak apically expanded to the diameter of the cylindrical nectary, the style apically darker, pubescent, the branches dark, ascending-pubescent; inner florets with corollas not exceeding the involucral bracts, yellow, glabrate, the anthers yellow, the appendages yellow, obtuse, basally tailed, the style branches scarcely darkened, ascending-pilose, the ovary larger than that of the outermost floret, less tuberculate, the nectary similar. *Achenes* all alike, yellowish, sulcate, apically tuberculate-barbed, the body ca. 3 mm long, the beak ca. 8 mm long, basally thickened and sulcate, terete above, basally broader; pappus of numerous, white, strigose bristles in several similar series surrounding the naked, flat beak apex.

This species may be recognized by its showy, yellow heads and beaked achenes. Native of the Old World, it is a near cosmopolitan weed, of frequent occurrence in temperate regions and in upland Chiriquí. The leaves are used in other countries for salads and for making wine. The immature heads have been pickled for a condiment or boiled as a vegetable, and the root has been used as a coffee adulterant. Latex of another Old World species has been used for rubber. The flowers are reported as a good nectar source for honey bees. This species is normally apomictic, and although showy with rich pollen and nectar rewards, plants are seldom fertilized by their frequent insect visitors. Outcrossing is exceptional. "Dandelion," "Diente de León."

CHIRIQUÍ: Boquete, *D'Arcy & D'Arcy 4659* (MO); *Dwyer 7041* (MO).

111. YOUNGIA

Youngia Cass., Ann. Sci. Nat. 23: 88. 1831. TYPE: *Y. lyrata* Cass. = *Y. japonica* (L.) DC.

Annual or perennial rosette *herbs*; pubescence of weak, uniseriate hairs; rooting by a taproot; sap milky. *Leaves* obovate or lanceolate, often runcinate or lyrate-dissected, sometimes dentate; distinct petiole often present. *Inflorescence* scapose, paniculate; peduncles slender, often pubescent; pedicels slender, subtended by scalelike bracts. *Heads* small, ligulate; involucre cylindrical, mostly glabrous, the bracts in 2 series, the outermost few, deltoid, short, mostly slightly overlapping, the innermost 6–12, lanceolate, twice as long or more than the outer series, thickening at the base in fruit; florets (5–)15(–30), all ligulate, all perfect, all fertile, the corolla yellow, the outer series sometimes dorsally reddish, the ligule with 5 short, sometimes reddish teeth, the tube apically pilose, the anthers with ill-defined appendages, basally tailed, style branches slender, puberulent, style apex pubescent. *Achene* compressed, ellipsoidal or lachrymiform, conspicuously many-ribbed, rugose; pappus of many fine, persistent, strigulose, white or buff bristles. *Pollen* echinolophate, 3-colporate. Base chromosome numbers $x = 5, 8$.

Youngia is a genus primarily Asian in origin with some three dozen species. It is often considered to be conspecific with *Crepis* L. Recognition of *Youngia* as a distinct genus is based on the work of Babcock & Stebbins (1937) who

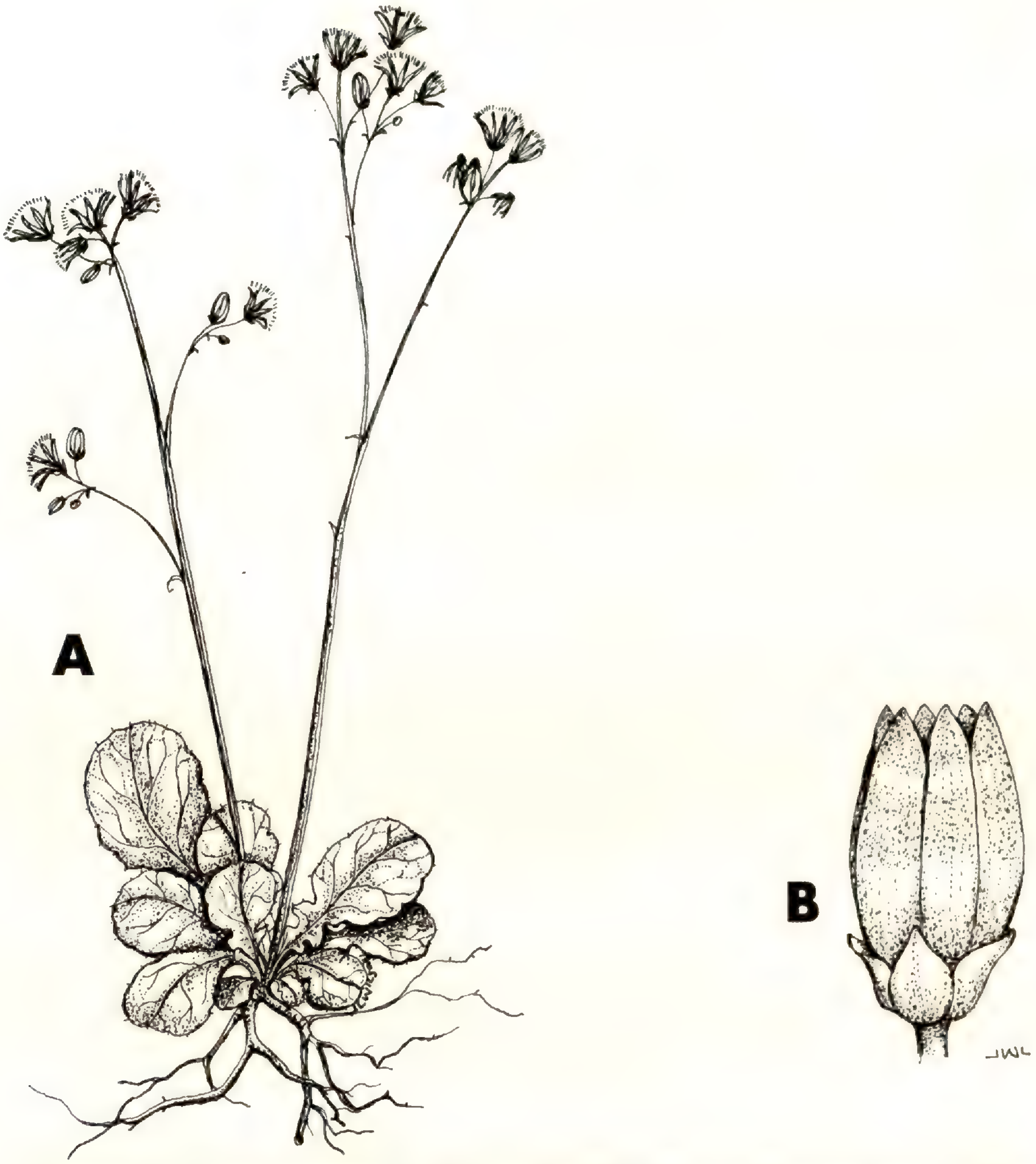

FIGURE 110. *Youngia japonica* (L.) DC.—A. Habit (× 9/10).—B. Unopened head (× 6 3/10). [After *D'Arcy & D'Arcy 6655* (MO).]

considered *Youngia* and *Crepis* to be only distantly related. In the Panamanian flora it is distinct by the milky sap, the involucral bracts in 2 series, the diminutive heads, and the scapose habit.

Literature:

Babcock, E. B. & G. L. Stebbins, Jr. 1937. The genus *Youngia*. Publ. Carnegie Inst. Wash. 484: 1–106.

1. **Youngia japonica** (L.) DC., Prodr. 7: 194. 1838.—FIG. 110.

Prenanthes japonica L., Mant. Pl. 107. 1767. TYPE: not seen.
Crepis japonica (L.) Benth., Fl. Hongk. 194. 1861.

Short-lived, mostly scapose *herb* to 50 cm tall; stems puberulent with long, multicellular hairs; rootstock short; sap milky. *Leaves* obovate, oblanceolate, or rotund, lyrate or runcinate, the terminal segment mostly rotund, apically rounded, dentate, crenate or entire, the basal portion narrowed into a narrow, wingless petiole, or with more or less deltoid segments, to 6(–25) cm long, the midvein often reddish, evenly pubescent overall. *Inflorescence* a scapose, several-headed panicle to 25 cm tall; peduncle glabrate, often reddish, slender, somewhat branched; pedicels filiform, ca. 5 mm long, subtended by scalelike bracts. *Heads* small, ca. 5 mm tall, slightly taller than broad; involucral bracts in 2 distinct series, the outer series of ca. 5, slightly imbricate or valvate, pinkish, deltoid bracts ca. 1 mm long, the inner series of ca. 8 lanceolate bracts ca. 6 mm long, glabrous, green with purplish costa, apically darkened, basally swollen in fruit, deflexed in age; receptacle flat, yellow, naked; florets all ligulate, all perfect, all fertile, the corolla yellow, 5–7 mm long, the ligule broad, the 5 short teeth darkened, the tube apically pilose, the anthers dark green, the appendages black, poorly defined, basally long-sagittate, the style apically pilose, the branches slender, pubescent, truncate, yellow. *Achene* brown, 2 mm long, compressed, ellipsoidal or conical, apically narrowed into an indistinct beak, many-ribbed, the ribs ascending-scabrid; pappus silky white of numerous, fine strigose bristles.

This species may be recognized by its diminutive size and the bright yellow corollas forming a disc only 3–4 mm across. It is a widespread weed of tropical and warm temperate regions, occurring in Panama in disturbed situations. Plants collected in Panama are smaller than those seen from Costa Rica.

CANAL ZONE: Summit Garden, *Croat 13475* (MO). CHIRIQUÍ: E side of Cerro Pando, 6000 ft, *D'Arcy & D'Arcy 6655* (MO).

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